Community phylogenetics and invertebrate herbivory in managed grasslands

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Chapter 1

GENERAL INTRODUCTION

GENERAL INTRODUCTION

Land-use change and intensification poses one of the major threats to biodiversity in terrestrial ecosystems now and for the next decades (Sala et al. 2000). To assess the consequences of ongoing and future biodiversity loss, it is crucial to understand the complex interactions between biodiversity and ecosystem functions. Biodiversity, however, is a fuzzy term that comprises different aspects of natural communities. So far, community species richness and functional diversity are two aspects of biodiversity that have received most attention in community ecology. Although these biodiversity measures have provided the predominant part of our knowledge on biodiversity – ecosystem relationships, advances in ecological theory and methods have revealed several shortcomings related to these approaches. In the past 20 years community phylogenetics has been proposed as an additional measure of biodiversity to enhance our understanding of the biodiversity – ecosystem functioning relationships (Webb et al. 2002a; Cavender-Bares et al. 2009; Srivastava et al. 2012). For example, phylogenetic diversity of plant communities has been shown to be a better predictor of productivity than species richness or functional diversity (Flynn et al. 2011). It has also been shown that phylogenetic diversity affects ecosystem processes. Herbivory in forests and grasslands was altered by phylogenetic diversity of plant communities (Parker et al. 2012; Dinnage 2013). Community phylogenetics also provide additional insights into community assembly processes compared to species richness or functional diversity. For example, Pellissier et al. (2014) showed that application of nitrogen and herbicides lead to a decrease in plant species richness, but promoted different responses in plant traits (specific leaf area and canopy height). Plant phylogenetic diversity increased when nitrogen and herbicides were applied together, most likely because traits that facilitate plant success under the applied conditions were not phylogenetically conserved. Dinnage (Dinnage 2009) showed that plant communities contain species that are closer related than expected by chance in plots that experienced higher disturbance, a pattern called phylogenetic under-dispersion or clustering (Webb et al. 2002a). Although most studies focus on primary producers in community phylogenetic analyses, these patterns apply also to animal communities as shown by Helmus et al. (Helmus et al. 2010). He analyzed zooplankton communities in disturbed lakes and found that communities in disturbed lakes contained more closely related species than in undisturbed lakes. Arthropod communities in general and in particular herbivorous arthropods, play a major role in ecosystem processes (Weisser and Siemann 2007). To date, however, our knowledge about the effects of land-use intensification on invertebrate herbivore communities, phylogenetic diversity of communities in particular, is still limited. Trophic interactions also play a major role in structuring insect communities. Dinnage et al. (2012) showed that increasing plant species richness and phylogenetic diversity increased arthropod diversity, insect herbivore diversity in particular. The relationships between plant and insect phylogenetic diversity yet remain largely unknown. Hence, understanding the effects of land use on phylogenetic diversity of plant and herbivore communities, as well as the relationships between plant and insect phylogenetic diversities, is crucial to predict the consequences of biodiversity loss on ecosystems.

To study the relationships mentioned above, an appropriate study system is of importance. This study was conducted within the Biodiversity Exploratories, a large-scale and long-term research project to study the relationships between land use, biodiversity and ecosystem functioning (Fischer et al. 2010). The Biodiversity Exploratories are situated in three regions in Germany (Schwäbische Alb in SW Germany; Hainich-Dün in Central Germany and Schorfheide-Chorin in NE Germany). Each of the regions comprises 300 experimental plots (150 in grasslands and 150 in forests) under constant land use. This study focuses on the grasslands which experience different levels and types of land use.

LAND-USE INTENSIFICATION AND PHYLOGENETIC DIVERSITY OF PLANT COMMUNITIES

Recent studies have shown that land-use intensification alters phylogenetic structure of communities in the way that they comprise species that are more closely related than expected by chance, a pattern called phylogenetic clustering (Dinnage 2009). The mechanism behind this pattern might be the environmental filtering, that is, selection of traits that enable species to cope with increasing land-use intensities (Webb et al. 2002a). But note that there are also other processes that might cause this pattern (Mayfield and Levine 2010). Other studies showed that land use can increase phylogenetic diversity of plant communities (Pellissier et al. 2014), a pattern that can occur when traits sensitive to the specific land use types are not phylogenetically conserved. Many important ecological traits are difficult to measure, or even still unknown. Because functional diversity is determining ecosystem functions and many traits are conserved along phylogenies, phylogenetic diversity has been proposed as a proxy for functional diversity (Cavender-Bares et al. 2009). Recent studies, however, showed that phylogenetic diversity is more a complement rather than a substitution to functional diversity (Bernard-Verdier et al. 2013). However, since phylogenies encompass the whole trait space of a community, phylogenetic diversity provides a single measure of diversity that can act as a better predictor of ecosystem functions than multidimensional functional diversity measures (Flynn et al. 2011). The contrasting results suggest that the responses of phylogenetic diversity to land use cannot be generalized. In addition, rather than a proxy for functional diversity, phylogenetic diversity should be considered as an additional measure that can enhance our understanding on the community level processes.

In the second chapter, I analyze the effects of land-use intensification on phylogenetic diversity of plant communities in temperate grasslands. In particular I test the assumption that land use leads to phylogenetic clustering of plant communities. The results show only a weak decrease of phylogenetic diversity in general, probably caused by a lack of phylogenetic conservatism in land-use sensitive traits as well as by regional peculiarities.

PLANT DIVERSITY AND LAND-USE EFFECTS ON INSECT HERBIVORE ASSEMBLAGES IN MANAGED GRASSLANDS

Invertebrates, in particular herbivorous insects, represent the most diverse group of animals and are involved in a plethora of ecological functions and processes (Weisser and Siemann 2007). Through the direct interactions with primary consumers, insect herbivores are especially closely linked to plants. Thus plant diversity should be a strong predictor of invertebrate herbivore diversity. Previous studies have found overall positive, but albeit sometimes weak relationships between plant and herbivore species richness (Root 1973; Haddad et al. 2009; Scherber et al. 2010a; Dinnage et al. 2012). Many insect herbivores feed on closely related plant species or clades (Weiblen et al. 2006; Futuyma and Agrawal 2009) probably because they share certain traits related to nutrition or other chemical processes that favor food specialization. Assessing plant traits that are related to host-plant utilization of herbivores can be difficult. In addition, other processes like biogeography of speciation and coevolution can create phylogenetic patterns in herbivore diets (Futuyma and Agrawal 2009), leading to idiosyncratic relationships between plant traits and herbivore feeding preferences (Dinnage et al. 2012). Phylogenetic diversity can overcome these shortcomings by providing a single measure of the available trait space in a plant community. It is therefore likely that plant phylogenetic diversity is a strong predictor of herbivore richness beyond plant species richness effects. In addition, due to the fact that many herbivores show a degree of phylogenetic specialization in their diets, increasing plant

phylogenetic diversity also should provide additional feeding niches to a greater number of herbivores. Thus, increasing plant phylogenetic diversity should lead to an increase not only in herbivore species richness but also in herbivore phylogenetic diversity through niche differentiation.

Not only biotic interactions between trophic levels affect diversity of insect herbivore communities, land-use intensification also decreases herbivore species richness in managed grasslands (Allan et al. 2014). Besides the direct effects of land use (e.g. mowing), plant diversity changes along land-use gradients might be the cause of insect herbivore richness decline. In addition to herbivore species richness, land-use intensification might also alter the phylogenetic structure of insect herbivore communities. For example, it has been shown that land-use intensification shifts the traits in butterfly communities to generalist characteristics (Börschig et al. 2013). If these traits show phylogenetic conservatism, i.e. closely related species resemble each other in these traits, the changes in land use intensity should also be reflected in the decreased phylogenetic diversity of butterflies. However, to date the effects of land use on phylogenetic diversity of insect herbivore assemblages has not been analyzed.

In the third chapter, I analyze the species richness and phylogenetic diversity of herbivorous insect communities (true bugs and butterflies) along gradients of plant diversity and land-use intensity. The results reveal a positive effect of plant species richness, but contrasting effects of plant phylogenetic diversity on insect herbivore species richness. Our results show no relationships between phylogenetic diversity of insect herbivores and land-use intensification or plant phylogenetic diversity. We suggest that lack of phylogenetic conservatism in land-use sensitive traits and clustered specialization of the herbivores might produce the detected patterns.

COMMUNITY PHYLOGENETICS AND ECOSYSTEM PROCESSES

Several ecosystem processes are influenced by community diversity (Sankaran and McNaughton 1999; Paquette and Messier 2011; Cadotte et al. 2012). Herbivory is an important process linking composition of plant communities and ecosystem functions such as productivity (McNaughton et al. 1989), decomposition (Cebrian and Lartigue 2004) and nutrient cycling (Belovsky and Slade 2000). Invertebrates are by far the most diverse and numerous group of herbivores. Although invertebrate herbivory in grasslands is relatively low (Unsicker et al. 2006), plants exhibit different anti-herbivorous defense mechanisms (Kessler et al. 2004), indicating that invertebrate herbivory might still be an important factor. So far, diversity of plant communities (Root 1973) and land use (Gossner et al. 2014) have been proposed as important determinants of invertebrate herbivory intensity.

Previous studies showed that plant species richness affected herbivory, but the direction of the relationships were opposing and seem to vary depending on the specific plant and herbivore communities analyzed (reviewed in Dinnage 2013). Moreover, several studies showed that plant species richness is a weak predictor of herbivory (Hanley 2004; Scherber et al. 2010b). Thus, other measures of plant diversity, such as functional or phylogenetic, have been proposed to enhance our understanding of the mechanics behind herbivory.

Most herbivores show a certain degree of specialization in their diets (Weiblen et al. 2006). They tend to feed on closely related plant species or clades probably because they prefer certain traits that are shared between closely related species or because of shared evolutionary history between herbivore and plant clades (Dinnage et al. 2012). Traits are often summed up to metrics of functional composition or diversity. Indeed, functional attributes of plant communities seem to be a better predictor of herbivory in grasslands than plant species richness (Scherber et al. 2010b).

Plant traits that are related to herbivory are supposed to be shared between close relatives. Determining and assessing those traits linked with herbivory, however, is not always straight forward. Knowledge which traits are actually predictors of herbivory is still scarce, but it seems that many of those traits include secondary metabolites that have to be

elaborately measured in the laboratory. Because of the overall conservative character of those traits in respect to evolutionary history (Wink 2003) and because a multivariate trait approach is needed to predict invertebrate herbivory (Loranger et al. 2012), it is reasonable to use community phylogenetic diversity as a proxy for phenotypic/trait diversity (Cavender-Bares et al. 2009). Several studies provided evidence that phylogenetic diversity is as strong predictor of herbivory (Parker et al. 2012; Dinnage 2013; Castagneyrol et al. 2014), however, opposing results on the direction of the relationships have also been reported (Hanley 2004; Scherber et al. 2006; Stein et al. 2010).

Herbivory is affected by biotic interactions, nevertheless, anthropogenic disturbance can also alter herbivory response. Land-use intensity has been shown to decrease herbivory in managed grasslands (Gossner et al. 2014). The interaction of land use and plant diversity suggests that beside direct effects, land use indirectly affects herbivory via changes in plant community diversity. Recalling the fact that phylogenetic diversity is a stronger predictor of herbivory than species richness, indirect effects are likely to be driven by changes in plant phylogenetic diversity.

In the fourth chapter, I test for the predictive power of plant species richness vs. plant phylogenetic diversity on invertebrate herbivory in managed grasslands. Further, I use structural equation modeling to test for the direct and indirect (*via* plant diversity changes) effects of land-use intensification. Overall, I found that phylogenetic diversity in an important predictor for herbivory and that although land use, in general, affects herbivory directly, regional differences in the effects call for caution in attempting to generalize the effects of land use on herbivory.

Chapter 2

DOES LAND-USE INTENSIFICATION DECREASE PLANT PHYLOGENETIC DIVERSITY IN LOCAL GRASSLANDS?

with Daniel Prati, Walter Durka, Stefan Michalski, Markus Fischer, Barbara Schmitt, Stefan Blaser & Martin Brändle

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ABSTRACT

Phylogenetic diversity (PD) has been successfully used as a complement to classical measures of biological diversity such as species richness or functional diversity. By considering the phylogenetic history of species, PD broadly summarizes the trait space within a community. This covers amongst others complex physiological or biochemical traits that are often not considered in estimates of functional diversity, but may be important for the understanding of community assembly and the relationship between diversity and ecosystem functions. In this study we analyzed the relationship between PD of plant communities and land-use intensification in 150 local grassland plots in three regions in Germany. Specifically we asked whether PD decreases with land-use intensification and if so, whether the relationship is robust across different regions. Overall, we found that species richness decreased along land-use gradients the results however differed for common and rare species assemblages. PD only weakly decreased with increasing land-use intensity. The strength of the relationship thereby varied among regions and PD metrics used. From our results we suggest that there is no general relationship between PD and land-use intensification probably due to lack of phylogenetic conservatism in land-use sensitive traits. Nevertheless, we suggest that depending on specific regional idiosyncrasies the consideration of PD as a complement to other measures of diversity can be useful.

INTRODUCTION

Land-use change is one of the primary drivers of biodiversity loss (Foley et al. 2005; Flynn et al. 2009). Despite a large amount of studies dealing with the effects of land use on biodiversity, there are still gaps in the understanding of land use – biodiversity relationships. For example, the negative effects of different land-use types on biodiversity can differ in strength or vary in their effects. In addition, regional idiosyncrasies might interact with land use and affect biodiversity responses to land-use intensification, thus impeding general predictions(Socher et al. 2012). Recent studies have advocated the consideration of phylogenetic diversity (PD) in ecological analyzes (Cadotte et al. 2008; Cavender-Bares et al. 2009; Vamosi et al. 2009; Srivastava et al. 2012). In brief, PD is defined as the total amount of phylogenetic space covered by species in a community. It therefore encapsulates the entire trait space of a community (Wiens et al. 2010) and thus, may serve as a complement to trait diversity if the traits cannot be measured or trait data are not available (Cadotte et al. 2008). Moreover, PD is an important factor for ecosystem function itself. It has been shown that PD can explain more variance in productivity in grasslands than species richness or functional diversity (Flynn et al. 2011). Plant productivity increased with mycorrhizal PD, which may be caused by niche differentiation, as increasing number of mycorrhizal families provide different advantages to their host plants (Maherali and Klironomos 2007). Higher plant PD also increases diversity of higher trophic levels and affects several ecosystem functions and processes (Dinnage et al. 2012; Cadotte et al. 2012; Dinnage 2013). That is, higher plant PD reinforces the positive effects of plant species richness on higher trophic levels when species richness is held constant (Dinnage et al. 2012). Finally it has been found that PD promotes ecosystem stability and resilience (Cadotte et al. 2012) as well as interacts with plant species richness and alters its effect on herbivory (Dinnage 2013). Despite a consensus that PD is an important factor in understanding biodiversity – ecosystem functions relationships (Srivastava et al. 2012) or community assembly rules (Mouquet et al. 2012), little effort has been done in analyzing the effects of land-use intensity on PD (Dinnage 2009).

In Central Europe managed grasslands are one of the most abundant and species-rich ecosystems (Pärtel et al. 2005). In Germany, about 12% of area is covered by grasslands (Statistisches Bundesamt 2012). Most of these grasslands were established during a long period of low-intensity land-use and a large number of species have adapted to those conditions causing high levels of biodiversity. Land-use intensification in particular during the 20th century posed considerable threats to biodiversity in

grasslands, e.g. due to dramatic habitat loss and extinction of less competitive species (Suding et al. 2005; Kleijn et al. 2009; Storkey et al. 2011). It is also likely that land-use intensification will be the major driver of biodiversity loss in grasslands during the next decades (Sala et al. 2000; Foley et al. 2005). To attain a compromise between high land-use intensity and biodiversity conservation (Foley et al. 2005) and to assess the consequences of biodiversity loss a deeper understanding of the relationship between land-use intensification, biodiversity and ecosystem functioning is mandatory.

In general previous studies of plant biodiversity-ecosystem functioning relationships have shown that species richness enhances ecosystem functions (Tilman et al. 1996; Hector et al. 1999; Cardinale et al. 2007). Simply counting the number of species, however, is often not sufficient for analyzing the effects of biodiversity on ecosystem functions (Cardinale et al. 2006). More comprehensive approaches consider functional diversity, defined as diversity of traits important for ecosystem level processes (Petchey and Gaston 2006). Functional diversity is thought to be the component of biodiversity with the largest effect on ecosystem processes (Tilman et al. 1997; Chapin III et al. 2000; Loreau 2000). However, implementation of trait data is subject to several limitations. For example, assessment of trait data is time-consuming and the *a priori* choice of specific traits is not always straightforward (Petchey and Gaston 2006). To overcome these shortcomings, PD has been proposed as a proxy for functional diversity (Webb et al. 2002a; Cavender-Bares et al. 2009). Recent studies, however, question PD as a proxy and propose it rather as a complement to functional diversity (Bernard-Verdier et al. 2013). Despite the current discussion on the use of community phylogenetics in analyzes of assembly processes under several biotic and abiotic conditions (Mayfield and Levine 2010) the importance of PD to ecosystem processes calls for its implementation into ecological analyzes (Cadotte et al. 2008). While the negative effect of land-use intensification on species richness and functional diversity has been subject to many studies (Díaz et al. 1999; Stevens et al. 2004; Flynn et al. 2009), a relatively small number of studies investigated how increasing land-use intensity affects PD of plant communities, particularly in grasslands. Studies that compared observed phylogenetic community structure of plants with expected patterns (Webb et al. 2002a) revealed shifts in phylogenetic community structure with increasing disturbance and stress (Knapp et al. 2008; Dinnage 2009; Kluge and Kessler 2011; Brunbjerg et al. 2012; Pellissier et al. 2014). Similar patterns were also shown within animal communities (Graham et al. 2009; Machac et al. 2011; Hoiss et al. 2012). Changes in phylogenetic community structure may include shifts from overdispersion, where co-occurring species are less phylogenetically related than expected by chance, to clustering, where co-occurring species are phylogenetically more related than expected by chance. Such a shift from overdispersion to clustering is thought to be caused by environmental filtering that selects species with similar ecological traits that are likely to be closely related (Dinnage 2009; Mayfield and Levine 2010; Brunbjerg et al. 2012). Increasing land use intensity should therefore favor plant species with traits adapted to cope with effects of land-use intensification like fertilization, cattle grazing and frequent mowing. If such traits are phylogenetically conserved and play a major role in the phylogenetic community assembly, communities are likely to become phylogenetically more clustered with increasing land-use intensity. If traits are convergent or show a low phylogenetic signal, plant communities should not exhibit phylogenetic clustering with increasing land-use intensities or even lead to an increase in PD (Pellissier et al. 2014).

For conservational purposes the response of rare species to land-use intensification is of great interest. Rare species are in general more vulnerable to land-use intensification than common species (Suding et al. 2005; Kleijn et al. 2009; Storkey et al. 2011). Assuming that common species might be better adapted to high land-use intensities, phylogenetic diversity of common species should be less sensitive to land-use intensification than that of rare species. However, to our knowledge there are no studies exploring the response of PD of rare and common species to land-use intensification separately.

Socher et al. (2012) showed that strength and direction of the effects of land use on biodiversity can differ between regions. Regional idiosyncrasies can also alter the effect of land use on phylogenetic diversity due to different regional species pools, environmental and geographical variables. It is

therefore necessary to compare the effects of land-use intensification on PD among regions. Other limitations of previous research on plant PD are that the majority of studies are either experimental or describe phylogenetic patterns along natural or environmental gradients and are restricted to certain, often narrow, taxonomic scales (Hector et al. 1999; Cavender□Bares et al. 2004). Descriptive studies of PD – land-use intensity relationships in human-disturbed systems are still scarce. When analyzing plant PD with respect to man-made disturbance, studies often focus on urban regions (Knapp et al. 2008) or do not encompass the most common agricultural land-use categories such as fertilization, mowing and grazing. Including most common land-use types in descriptive studies of PD – land use relationships in agricultural systems could give new insights on these relationships under "real world" conditions. Previous studies may also suffer from the lack of considering species abundance data. Presence/absence data are highly sensitive to the chance and possible temporary occurrence of a single individual in unusual or unsuitable habitat. Interspecific relationships and interactions between species and ecosystems are based on interactions between individuals, which are cumulative in their effects. Neglecting abundance data may impede to discover important ecological relationships (Vamosi et al. 2009).

In this study we use species abundance data to analyze the PD of plant communities in local grasslands (150 sites) across land-use intensification gradients in three regions in Germany. In particular we aimed to answer the following questions:

1) Are there regional differences in the response of phylogenetic diversity to land use?
2) Does land-use intensification decrease phylogenetic diversity of plant communities in grasslands?
3) Does phylogenetic diversity of common and rare species assemblages show different relationships with respect to land-use intensification?

For a better understanding and interpretation of the relationship between PD and land-use intensification, information on the phylogenetic signals in traits relevant for land use are of interest (i.e. related to a certain ecosystem function or environmental gradient). Thus, we used a set of traits that are likely to be sensitive to land use and tested for phylogenetic signal in those traits.

METHODS

STUDY AREA

Our study is part of the Biodiversity Exploratories project, a large German research project to investigate the relationships between land-use, biodiversity and ecosystem functioning (www.biodiversity-exploratories.de). The Biodiversity Exploratories represent three typical regions in Germany covering a south-west – north-east gradient and each region comprises grasslands and forests under a range of land-use types and intensities (Fischer et al. 2010). The exploratory Schwäbische Alb (hereafter named Alb) is situated in the SW Germany and is part of the UNESCO Biosphere Reserve Schwäbische Alb. The exploratory Hainich-Dün (hereafter named Hainich) is situated in western Thuringia, central Germany. The exploratory Schorfheide-Chorin (hereafter named Schorfheide) is situated in NE Germany and is part of the UNESCO Biosphere Reserve Schorfheide-Chorin. In each region 50 experimental grassland plots representing gradients from semi-natural to intensive land-use were established (overall 150 plots). For more details see (Fischer et al. 2010).

LAND-USE

Land-use information for each of the 150 grassland plots was obtained by yearly interviews with farmers and land-owners between 2006 and 2010. The acquired information included fertilization level (kg nitrogen ha^{-1} $year^{-1}$), mowing frequency (number of cuts $year^{-1}$) and grazing intensity (livestock units x days of grazing ha^{-1} $year^{-1}$) (Fischer et al. 2010). The three land-use components were standardized by the respective mean intensity within each region to yield the fertilization, mowing and grazing intensity. For each year the individual components were summed up to a combined quantitative land-use intensity index (LUI). The yearly LUI-values (2006-2010) were averaged for each plot and the obtained means were then used in all our analyses (Blüthgen et al. 2012).

VEGETATION RELEVES AND PHYLOGENY

Between 2009 and 2011 we recorded the vegetation on a 4 x 4 m plot in each of the 150 grasslands three times (2009, 2010 and 2011). For each plot, vascular species richness and their relative abundance in percent cover was estimated. The species were further grouped into common and rare species based on their abundance for each year and region separately, taking into account local (plot) abundance and distribution (number of plots occupied) of each species. Common species were defined as the top 10% in terms of total abundance across plots occupied by a species, while the bottom 90% of the species was defined as rare. Based on these data we calculated the species richness of all, common and rare species as the average richness per plot across the three years. Note that the analyses of plant species richness from our study sites have been already published elsewhere (Socher et al. 2012; Allan et al. 2014). We included these results here only for comparative purposes. Therefore our discussion focuses only on the effects of land-use on PD. A low number of gymnosperms and ferns with low site incidence were omitted from all analyzes.

Phylogenetic relatedness of species was obtained from a well resolved and dated phylogeny of the Central European flora (Durka and Michalski 2012). In brief, this phylogeny was assembled by manually grafting subtrees on a backbone topology, dating of nodes based on fossil records using the bladj algorithm in PHYLOCOM (Webb et al. 2008) and calculating an ultrametric tree (for details see Durka and Michalski 2012). We pruned the overall phylogeny to match the species pool of each of the three regions. As a result we obtained three trees, one for each region, representing the phylogenetic relationships of the respective species pool.

According to the data sharing regulations of the Biodiversity Exploratory Project and in accordance with the rules of the German Science Foundation DFG, the data will be made publicly available no later than five years after collection

TRAITS AND PHYLOGENETIC SIGNAL

We compiled functional trait data from different data bases. As traits related to productivity we included the maximal plant height (cm) and specific leaf area (SLA; in cm2/g). As traits related to reproduction we used data start of flowering (month of the year). Data on the SLA were taken from the LEDA trait data base (Kleyer et al. 2008), data on start of flowering and plant height were gathered from BiolFlor data base (Klotz et al. 2002) and from floras (Binz and Heitz 1990; Jäger and Werner 2005). Means were calculated when entries differed among the sources, but generally the values were highly consistent across sources. We further compiled performance and persistence traits relevant for agricultural grasslands: (1) soil nutrient indicator value (N, (Ellenberg et al. 1992), (2) mowing tolerance (M), (3) grazing tolerance (G) and (4) trampling tolerance (T, all according to (Briemle and Ellenberg 1994) from (Briemle et al. 2002) and Briemle pers. comm.). For all traits we hypothesized that different agricultural use, in particular fertilization, mowing and grazing selects for species with different traits values. All indicators have numeric values ranging from 1 (low) to 9 (high). Available trait data ranged from 77% (SLA, height and flowering onset) to 86% (G) of the species.

We tested for the strength and significance of phylogenetic signals in traits using Pagel´s λ and Blomberg's K implemented in the phytools package (Revell 2012) in R. We log transformed values for the maximum height to achieve normality. It has been proposed that Pagel´s λ is an overall more robust metric than e.g. Blomberg's K (Münkemüller et al. 2012), however, in general both metrics revealed similar results.

PHYLOGENETIC DIVERSITY

Phylogenetic diversity estimates of plots were calculated with the "picante" package in R (Kembel et al. 2010). We calculated for each year and region separately the mean pairwise distance (MPD) and mean nearest taxon distance (MNTD) (Webb et al. 2002a) weighted by species abundance (estimated % cover) as well as using presence/absence data. Considering % cover as a surrogate for species abundance may only approximate the "true" species abundance distribution within a community. However because of the large number of plots in our study individual counts of species would be very time-consuming and are thus not feasible. Estimates of % cover are at least rough approaches to estimate abundance and we suggest that analyses based on such approaches are more meaningful than

considering only presence/absence data, especially in the context of the relative contribution of abundant, subordinate and transient species (Grime 1998). We used a slightly modified calculation of MPD based on abundance data as proposed by Gerhold et al. (Gerhold et al. 2013) to reduce effects of species richness. Abundance weighted and presence/absence versions of indices showed moderate correlations (MPD: $r = 0.41$; MNTD: $r = 0.58$). However, results based on the two indices did not differ considerably and therefore we present here only the results of abundance weighted indices (see Appendix S5 and S6 for presence/absence PD results).

MPD measures the mean phylogenetic distance between two taxa in a sample and MNTD the mean phylogenetic distance to the nearest taxon in a sample. Hence MPD summarizes all phylogenetic distances including those of very distantly related species (e.g. between species of different orders) while MNTD considers only those between the most closely related species (e.g. between species within a genus). Thus, a stronger relationship of MNTD with land-use intensity compared to MPD would indicate that land-use has a stronger effect on the terminal than on the basal phylogenetic composition of a community. Both metrics depended on species richness and we therefore calculated standardized effect sizes [(observed metric - expected metric) / standard deviation of expected metric)]. We used a null model that shuffles the tip labels of the phylogeny maintaining all other properties of the sample matrix (i.e. species richness in plots and species prevalence). This null model was chosen since it tests for the null hypothesis, that phylogeny is not an important factor for structuring plants communities. Note that effect sizes of both metrics were calculated for each year and region separately. For each plot we then calculated averages across the three years which were further used in all subsequent analyses (see above).

We used simple linear regressions and ANOVAs to analyze the relationships between plant PD and land-use intensification. We considered region (exploratory) as a factor to analyze whether PD differs among regions and whether the relationships

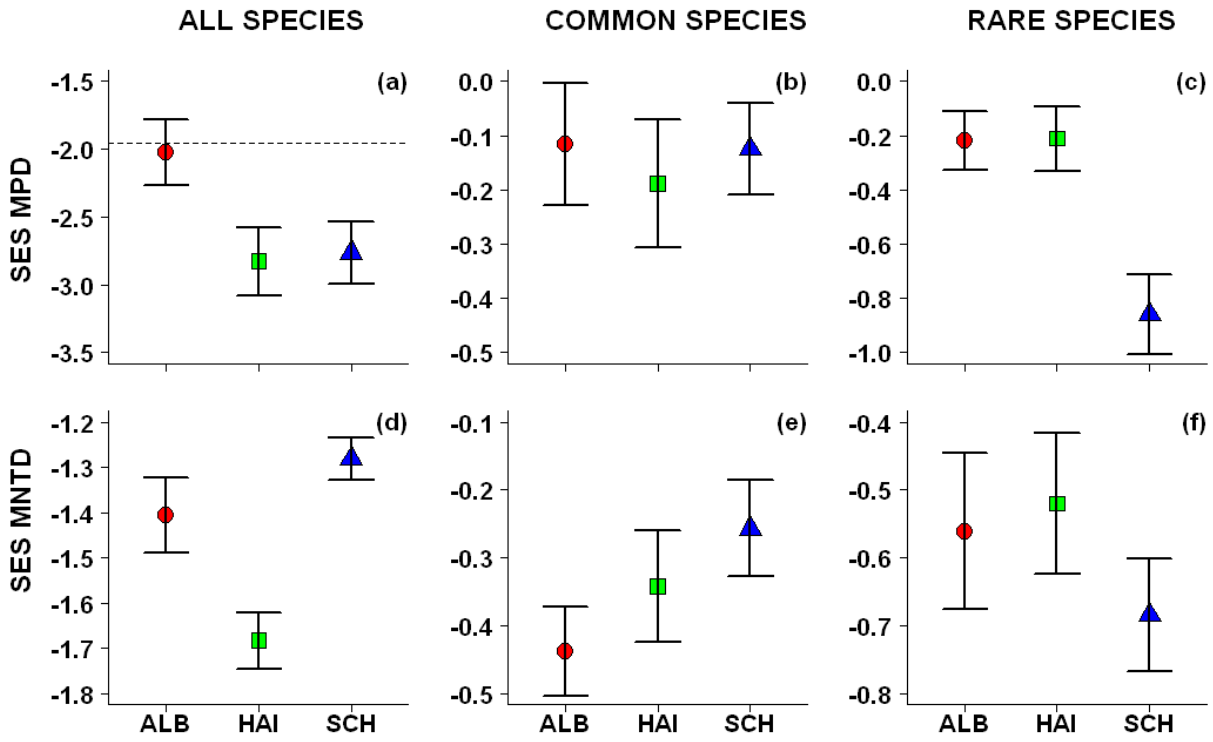

Figure 1. Mean (±SE) values of MPD and MNTD effect sizes for total, common and rare species assemblages in three regions in Germany.

(a)-(c) Mean MPD and (d)-(f) mean MNTD for all, common and rare species assemblages in the three regions. Region abbreviations: ALB = Schwäbische Alb (red circle); HAI = Hainich-Dün (green square); SCH = Schorfheide-Chorin (blue triangle). Error bars indicate ± SE. Points below the dashed line (< -1.96) are significantly clustered. Note different scales of y-axes.

between PD and LUI differ among regions (region x LUI interaction). To assess whether rare species assemblages respond more strongly to increasing land use than common species, we compared the slope of the regression lines with an ANCOVA by testing the significance of the LUI x "rarity" interaction. All statistical analyses were conducted in R (R Core Team 2014).

Results

A total of 282 vascular plant species were recorded in the three regions from 2009 to 2010 (Appendix S1). We found depending on the considered species pool and the specific traits analyzed varying levels for Pagel´s λ and Blomberg's K (Appendix S2). Based on Blomberg's K we found no strong phylogenetic conservatism in analyzed traits (Appendix S2). This suggests that PD cannot be seen as an overall proxy for functional diversity along land-use gradients.

Average total, rare and common species richness differed among regions (Appendix Table S3). Total and rare species richness decreased with increasing LUI with regional effects modulating the response of. In two regions (Alb, Hainich) total and rare species richness decreased with increasing LUI while in Schorfheide no effect was observed. The relationship between common species and LUI showed very contrasting patterns between regions but there was no overall decrease in species richness (Appendix S3).

Overall, average PD strongly varied among regions. But note that the differences depended on the PD-metric used and whether rare/common species were considered (Fig. 1a-f). When all species were considered, effect size of MPD showed strong significant clustering of communities in two regions (Hainich and Schorfheide) while MNTD estimates showed random patterns in all three regions. Mean phylogenetic community structure was random in respect to phylogeny for common and rare species assemblages in all three regions. After accounting

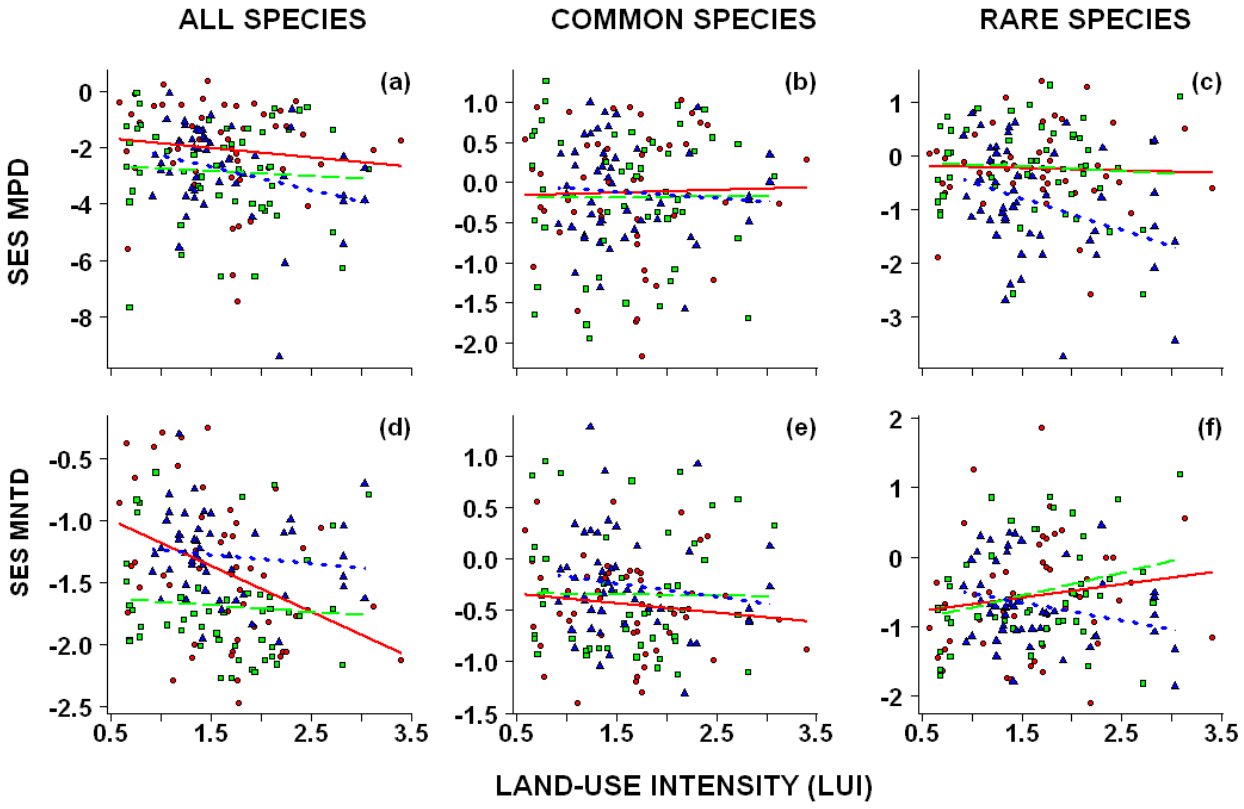

Figure 2. Relationships between mean pairwise distance (effect size MPD), mean nearest taxon distance (effect size MNTD) and land-use intensity (LUI) in three regions in Germany.
Linear regression plots showing regression slopes for relationships between (a-c) mean pairwise distance and (d-f) mean nearest taxon distance for total, common and rare species assemblages and land-use intensity (LUI). Color and type code: red solid line/circle = Schwäbische Alb; green dashed line/square = Hainich-Dün; blue dotted line/triangle = Schorfheide-Chorin. Note different scales of y-axes. For significance of regression slopes see Appendix S4.

for regional differences, total species MNTD decreased with increasing land-use intensity while MPD showed only a marginally significant decrease with similar relationships in all three regions (Tab. 1). Furthermore, land-use had slightly different effects on MNTD depending on region indicated by a marginally significant region x LUI interaction (Tab.1), with a stronger decline of MNTD in one region (Alb: $r = -0.39$, $p < 0.01$, Appendix S4), in particular. The other two regions showed a non-significant negative trend (Fig. 2). For MPD, only one region (Schorfheide) showed a significant decline with increasing land-use intensity ($r = -0.3$, $p < 0.05$; Fig. 1, Appendix S4).

In general we found that for both common and rare species PD was not or only weakly affected by increasing land-use intensity. The relationships did not vary among regions except for rare species MPD (Tab. 1, Fig. 2). Overall, the strength of phylodiversity – land-use intensity relationships did not differ between common and rare species assemblages over three regions as indicated by non-significant LUI x rarity interaction terms in our models (Tab. 2).

Discussion

Land-use intensification is one of the major threats to global biodiversity in grasslands (Sala et al. 2000). However, only a few studies have analyzed the effects of anthropogenic influence on PD of grassland plant communities. Several studies showed that anthropogenic influence can cause a decline in PD of species communities (Knapp et al. 2008; Dinnage 2009; Helmus et al. 2010) which possibly may also decrease trait diversity and associated ecological functions (Srivastava et al. 2012). In particular, PD can be important for ecosystem functioning when the ultimate processes, which depend on plant traits and trophic interactions, show a phylogenetic signal (Srivastava et al. 2012). It has been shown that in grasslands PD can act as a better predictor of productivity than species richness or functional diversity (Cadotte et al. 2009; Flynn et al. 2011). Moreover, herbivory was stronger related to phylogenetic relatedness than to plant functional traits (Paine et al. 2012). An experimental study by Pellissier et al. (2014) revealed an increase in PD after strong fertilization and herbicide application while functional traits showed contrasting relationships presumably by selecting for convergent traits. We found no evidence for strong phylogenetic signal in selected land-use sensitive traits (Appendix S2). Thus, phylogenetic diversity may not capture the relevant functional information leading to a relatively weak response to land-use intensification (Bernard-Verdier et al. 2013). On the other side, the significant decrease of PD depending on region and metric used (see below), shows that PD might capture additional information beside the measured traits.

Dinnage (Dinnage 2009) showed that the phylogenetic structure of plant communities in disturbed plots of old field sites is more clustered than expected, whereas phylogenetic structure in undisturbed plots does not differ from random expectations. This indicates, that land-use might act similarly to environmental filters and select for (presumably closely related) species with similar traits, which enable species to cope with disturbance. However, Dinnage analyzed the vegetation of an old field system with plowing being the disturbance that affected the phylogenetic diversity. This kind of disturbance mediates phylogenetic succession which can lead to increasing phylogenetic clustering of plant communities (Valiente-Banuet and Verdú 2007). Our study sites are exposed to land-use types completely different to the former study and our results differ in the strength of the PD response to land-use intensification. Although land-use

Table 1. Summary of linear models. Effects of region, land-use intensity (LUI) and its interaction with region on effect size of (A) mean pairwise distance (MPD) and (B) mean nearest taxon distance (MNTD) for total, common and rare species assemblages in the three regions in Germany. ANOVA table with F and *p* values of the full models. Significant values in bold.

A		MPD (total)		MPD (common)		MPD (rare)	
	df	F	*p*	F	*p*	F	*p*
Region	2	3.44	**0.035**	0.14	0.87	9.04	**0.0002**
LUI	1	3.65	0.06	0.01	0.91	3.71	0.06
Region x LUI	2	0.68	0.51	0.12	0.89	2.15	0.12
Residuals	144						

B		MNTD (total)		MNTD (common)		MNTD (rare)	
	df	F	*p*	F	*p*	F	*P*
Region	2	10.43	**<0.001**	1.51	0.22	0.73	0.48
LUI	1	7.6	**0.0066**	1.13	0.29	1.33	0.25
Region x LUI	2	3.02	0.052	0.25	0.78	3.51	**0.032**
Residuals	144						

intensification slightly decreased phylogenetic diversity, considering the mean nearest taxon distance (MNTD) in particular, it did not lead to a shift form random to clustered community structures (Tab.1, Fig. 2). In general, plant communities exhibited clustered and random phylogenetic structures on plots with both, low as well as high land-use intensities (points <1.96 on y-axis; Fig. 2). There are factors causing clustering of communities, especially when considering the tree-wide patterns (MPD, Fig. 1a) as was shown in several studies (e.g. Cavender-Bares et al. 2009; Kluge and Kessler 2011). Whether these factors refer to environmental filters (Butterfield et al. 2013; Culmsee and Leuschner 2013) or exclusion of weak competitors (Mayfield and Levine 2010) we cannot distinguish in our study. Land-use intensity, however, seems to play a minor role as determinant of phylogenetic community structure of plants in grasslands. This is contrary to the results of Dinnage (Dinnage 2009) but such differences might be caused by different land-use types, with plowing causing a strong disturbance within habitats compared to our land-use types. Note also that in Dinnages study no gradient of land-use intensity was analyzed and the definition of regional species pools was different from our study. Nevertheless, the slight decline of PD in our study may indicate that the influence of factors causing phylogenetic clustering of communities is mediated through or caused by increasing land-use intensity.

Table 2. Summary of linear models. Values for t-statistics and corresponding p values of the linear models with (A) MPD and (B) MNTD as dependent variables and LUI, rarity (two-level factor: common and rare) and their interaction as independent variables. Interaction term determines whether rare species PD response differs from that of common species PD. ALL: three regions combined; ALB: Schwäbische Alb; HAI: Hainich-Dün; SCH: Schorfheide-Chorin. Significant values in bold.

A	MPD							
	ALL		ALB		HAI		SCH	
	t	*p*	t	*p*	t	*p*	t	*p*
Intercept	-0.65	0.52	-0.55	0.58	-0.61	0.54	0.04	0.97
LUI	-0.1	0.92	0.19	0.85	0.03	0.98	-0.42	0.67
Rarity	0.25	0.8	0.04	0.97	0.29	0.77	0.19	0.85
LUI x Rarity	-1.39	0.17	-0.3	0.77	-0.36	0.72	-1.8	0.08

B	MNTD							
	ALL		ALB		HAI		SCH	
	t	*p*	t	*p*	t	*p*	t	*p*
Intercept	-1.58	0.12	-1.09	0.28	-1.3	0.2	-0.21	0.83
LUI	-0.87	0.38	-0.61	0.55	-0.08	0.94	-0.98	0.33
Rarity	-2.61	**0.009**	-1.57	0.12	-2.08	**0.041**	-0.66	0.51
LUI x Rarity	1.52	0.13	1.33	0.19	1.69	0.09	-0.72	0.47

Many studies dealing with phylogenetic community structure use only one phylogenetic diversity index like NRI or NTI (equivalent to [-1 * effect size MPD] and [-1 * effect size MNTD], respectively) (e.g. Kluge and Kessler 2011; Münkemüller et al. 2012). Since the two metrics measure PD at different depths of phylogeny, with MPD (NRI) capturing tree-wide patterns and MNTD (NTI) being more sensitive to the tips of a phylogeny (Webb et al. 2002a), depending on the distribution of traits, results of analyses might differ. However, when both metrics were used, similar results were reported (Culmsee and Leuschner 2013). In our study, although the two metrics showed similar relationships with land use, MNTD was more sensitive to increasing land-use intensity. This emphasizes the importance of including different indices into analyzes of PD, as land-use sensitive traits might be conserved within a few relatively young clades (e.g. within families) and thus might be masked when using metrics considering a broader phylogenetic scale (e.g. MPD). Because MNTD shows a stronger response to land-use intensification it is possible that those traits are conserved in the younger nodes of phylogeny. Thus, using MPD might not capture relevant trait information when analyzing the effects of land use on phylogenetic diversity. In fact, as Blomberg's K can be thought of as the partitioning of variance with low values (K<1) indicating variance within clades, this might be the reason for MNTD being more sensitive to land use.

Although common and rare species might differ in several traits (Farnsworth 2007) or their sensitivity to soil biogeochemical parameters (Kleijn et al. 2008) and respond differently to land use and competition (Dawson et al. 2012), we found no significant differences in their response to increasing land-use using analysis of covariance (Fig. 2, Tab 2). This suggests that traits that probably affect the abundance of species are randomly distributed across our plant phylogeny or/and are not affected by land-use. The only trait that was relatively strong conserved in both, common and rare species was maximum height. Despite a relatively high phylogenetic signal in this trait, it seems that height is not a strong determinant of phylogenetic community structure in both, common and rare species assemblages. Another explanation might be that PD of common and rare species might respond differently to the single LUI components due to

different traits not accounted for in our study and combining those to one index might neglect the differences in strength and direction of responses. Likewise, as the effects of land-use on PD did not differ in general between common and rare species communities, but rather showed slightly different patterns on a smaller scale, they should be examined separately if conservation efforts attempt to increase diversity for endangered taxa.

It is well known that regional peculiarities and species pools influence regional phylogenetic diversity (Anacker and Harrison 2012; Blanchet et al. 2013). For our study regions we found that considering all species Alb had overall high and Hainich overall low PD. Schorfheide showed contrasting patterns depending on the PD-metric used. Low MPD values suggest, that species in communities are closely related when accounting for the whole phylogeny, but high MNTD values indicate, that on lower phylogenetic scales (e.g. within families) species are distantly related. This might be explained by the fact that Schorfheide was more strongly affected by the Pleistocene glaciations than the other regions. One may argue that the plant communities of Schorfheide are still dominated by ecologically similar species belonging to closely related higher clades. Environmental filtering is then likely to cause strong phylogenetic clustering of communities considering the MPD (Fig. 1a). By contrast, within these clades PD might have increased due to limiting similarity (MacArthur and Levins 1967) causing random community structure (Fig. 1d).

Differences in PD among regions may, to some extent, be also due historical land use rather than current as suggested for species richness or functional diversity (Anacker and Harrison 2012; Klaus et al. 2013). Such regional differences call for a careful consideration of regional particularities when providing management strategies to maintain or increase phylogenetic diversity of grassland plant communities under “real world” conditions.

The theory behind phylogenetic patterns along disturbance gradients relies on several hypotheses about distribution of ecological traits across phylogenetic trees (Webb et al. 2002a; Losos 2008; Cadotte et al. 2009; Mayfield and Levine 2010; Flynn et al. 2011). We showed that although potentially land-use relevant traits show some levels of phylogenetic conservatism, PD still can provide additional information. The consideration of PD is therefore in particular important in situations when functional traits of species are not available. Phylogenetic methods can complement ecological analyzes, but it must be pointed out that PD cannot be seen as a surrogate for other biodiversity metrics, functional diversity in particular.

Chapter 3

DOES EVOLUTIONARY HISTORY INFLUENCE THE RELATIONSHIP BETWEEN INSECT AND PLANT DIVERSITY IN MANAGED GRASSLANDS?

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ABSTRACT

Niche theory predicts an enhanced diversity of insects with increasing plant diversity. This should be most pronounced in interacting primary consumers such as herbivorous insects. In previous studies the strength of the relationship, however, varied suggesting that additional factors such as the phylogenetic composition of assemblages or environmental pressures (e.g. disturbance or land use) may be important. In this study we first analyzed the relationships between herbivorous insect species richness, i.e. true bugs and butterflies, and phylogenetic diversity of plants and land-use intensification at 150 managed grasslands sites across three regions in Germany. Second, we analyzed relationships between phylogenetic diversity of true bug and butterfly assemblages and phylogenetic diversity of plants as well as land-use intensity. Plant phylogenetic diversity, had no consistent positive effects on herbivore species richness after accounting for the effects of plant species richness. There were no relationships between herbivore phylogenetic diversity and both, plant phylogenetic diversity and land-use intensity. Our results suggest that plant phylogenetic diversity does not explain additional variance in herbivore diversity beyond the effects of plant species richness. Further, land-use intensification has no effect on the phylogenetic community structure of insect herbivore assemblages. We suggest that clustered specialization of different insect taxa on certain clades within the plant phylogeny may cause the poor relationship between herbivore species richness and plant phylogenetic diversity or plant and insect phylogenetic diversity.

INTRODUCTION

A decline of consumer diversity caused by a loss of plant diversity has been frequently observed (Siemann 1998; Haddad et al. 2009) and thus, the latter measure has been widely used as a predictor of the former (Dinnage et al. 2012). One hypothesis that can explain the positive relationship between plant and herbivore diversity is the Resource Specialization Hypothesis (Hutchinson 1959). Implying that many herbivores are food specialists to some degree (Weiblen et al. 2006; Futuyma and Agrawal 2009), species rich plant communities might provide additional food niches to a higher number of herbivores compared to species poor plant communities. Indeed, Haddad et al. (Haddad et al. 2009) found a strong positive relationship between herbivore and plant species richness. In addition, functional groups represented in the plant communities such as grasses, herbs and legumes had strong effects on herbivore richness and abundance, which supports the Resource Specialization Hypothesis (Haddad et al. 2009).

Herbivores tend to feed on closely related plant species or plant clades (Weiblen et al. 2006) that presumably share specific traits (e.g. nutrient content, palatability). Phylogenies integrate these and even unmeasured or unknown traits into one measure (Srivastava et al. 2012). Thus, phylogenetic diversity should act as a strong predictor of herbivore diversity, i.e. higher plant phylogenetic diversity should increase herbivore richness via provision of additional niches for herbivores. Indeed, it has been shown that plant phylogenetic diversity strongly increases herbivore richness and abundance. In addition, phylogenetic diversity interacts with plant species richness resulting in a stronger effect of species richness when phylogenetic diversity is high (Dinnage et al. 2012). Because closely related species resemble each other, it is likely that closely related herbivore species feed on closely related host plant species or clades. Increasing plant phylogenetic diversity should therefore also be reflected by increasing phylogenetic diversity of associated herbivore communities. Plant phylogenetic diversity is likely to increase insect herbivore diversity (taxonomic and phylogenetic) beyond the effects of species richness.

Herbivore diversity is not only affected by plant diversity. For example, land-use intensification decreases species richness of arthropod communities in managed temperate grasslands, mainly through land-use induced decrease in plant diversity (Simons et al. 2014a). It is also possible that land use leads to a non random loss of species by selecting for certain

traits that enable these species to cope with increasing land-use intensities or decreased plant taxonomic and phylogenetic diversity.

True bugs (Hemiptera, Heteroptera) and butterflies (Lepidoptera, Rhopalocera) are two groups of herbivorous insects that have been shown to be good indicators of changes in consumer communities along disturbance and plant diversity gradients. Heteroptera respond quickly to environmental and land-use changes (Morris 1979; Morris 1990; Brändle et al. 2001; Simons et al. 2014a) and are affected by several attributes of vegetation (Sanderson et al. 1995; Frank and Kunzle 2006; Torma et al. 2010). Further, they are an overall good indicator of the total arthropod diversity in agricultural ecosystems (Duelli and Obrist 1998). Butterflies interact with plants by feeding on plants as larvae and acting as flower visitors as adults. They also have a relatively narrow host range as larvae and feed on certain closely related species (Fordyce 2010; Vila et al. 2011). Land-use change has a negative effect on butterfly diversity in grasslands and causes changes in functional composition (Börschig et al. 2013).

From theory outlined above we derived three expectations: First we expect plant phylogenetic diversity to explain additional variance of herbivore diversity after accounting for the effects of plant species richness. Second, we expect a positive relationship of herbivore phylogenetic diversity with plant phylogenetic diversity. Third, we expect a decrease of herbivore species richness and phylogenetic diversity with increasing land-use intensity. To test our expectations we use a comprehensive dataset of plant and insect communities on a total of 150 grassland plots subjected to various levels of land-use intensities across three regions in Germany.

METHODS

STUDY AREA AND SITES

The study was conducted within the Biodiversity Exploratories project (www.biodiversity-exploratories.de) in three regions in Germany comprising regional-specific ranges of land-use types and intensities in grasslands (Fischer et al. 2010). The Schwäbische Alb (hereafter Alb) is situated in the SW Germany and is part of the UNESCO Biosphere Reserve Schwäbische Alb. The Hainich-Dün (hereafter Hainich) is situated in western Thuringia, central Germany and includes the national park Hainich. The Schorfheide-Chorin (hereafter Schorfheide) is situated in NE Germany and is part of the UNESCO Biosphere Reserve Schorfheide-Chorin. Climatic and geological variables differ between the three regions (Schwäbische Alb; 460–860 m a.s.l., 48°43′ N 9°37′ E, 6-7° C annual mean temperature (a.m.t.), 700-1000 mm annual mean precipitation (a.m.p.); Hainich-Dün: 285–550 m a.s.l., 51°20′ N 10°41′ E, 6.5-8° C a.m.t., 500-800 mm a.m.p.; and Schorfheide Chorin: 3–140 m a.s.l., 53°02′ N 13°83′ E, 8-8.5° C a.m.t., 500-600 mm a.m.p.). In each region, 50 experimental grassland plots ranging from semi-natural to intensive land use were established (overall 150 plots).

LAND-USE INTENSITY

Land-use information was obtained between 2006 and 2010. For all plots we used a continuous land-use intensity index (LUI) summarizing three different land-use types (mowing, fertilization and grazing). Due to variability of land-use intensities between the years, we used the mean between all years to better cover the variation in land use. For more details about study sites and land use see Fischer et al. (2010) and Blüthgen et al. (2012).

PLANT DIVERSITY

Plant diversity data (species richness and phylogenetic diversity) were taken from a previous study on plant phylogenetic diversity and land-use intensification in the same study sites (Egorov et al. 2014). Plant phylogenetic diversity was calculated from a total of 282 plant species in the three regions. The complete phylogenetic tree of all plants was pruned to match the region-specific species pools. Mean pairwise distance (MPD) and mean nearest taxon distance (MNTD) were calculated. We used both, presence/absence and abundance data to calculate the phylogenetic diversity. However, since the results for the main questions did not differ between the both approaches, we present the presence/absence based results. Standardized effect sizes of phylogenetic diversity indices were calculated and used in the following analyzes to

reduce the effect of species richness on phylogenetic diversity. Phylogenetic diversity was calculated using the *picante* package (Kembel et al. 2010) in R (R Core Team 2014).

Species sampling and molecular methods

Heteroptera specimens were sampled on all 150 plots in the three regions using sweep-netting with a total of 60 double sweeps along three plot border transects twice a year (June and August) in the years 2008 to 2011 (for further details see (Simons et al. 2014b; Simons et al. 2014a)). Samples were transferred to 70% ethanol in the field. Butterflies were surveyed from May to August 2008 along fixed transects on 137 plots by sweep-netting (for further details see Börschig et al. 2013).

True bug specimens were separated from other arthropods and plant material in the laboratory. All adult specimens were subsequently identified to the species level by taxonomic specialists and stored in 70% ethanol. Butterflies were identified in the field and released. For several specimens identification in the field was not possible and they were taken to laboratory for further identification.

We constructed a true bug phylogeny using DNA sequences from NCBI (GenBank) and a recent barcoding project (Raupach et al. 2014). Additionally, for species where sequences were not available, DNA was extracted either from legs and/or hemelytra from ethanol-preserved or dry specimens from the project reference collection using the DNeasy Blood & Tissue Kit from QIAGEN. For a few species specimens of private collections were used. On these samples, we followed already published protocols (Schuh et al. 2009; Li et al. 2012) and amplified the regions 18s and COI. We used the primer pairs 3F-18 Sbi and 5F-9R for 18s RNA amplification (Schuh et al. 2009) and the primer pair LCO1490 and HCO2190 for COI amplification (Folmer et al. 1994).

We retrieved all butterfly sequences from NCBI, and we constructed a phylogeny based on six regions: EF1-alpha, Wgl, 16s rRNA, COI, NDH1 and NDH5 (see Pellissier et al. 2013a for further details).

Phylogeny reconstruction

We constructed ultrametric phylogenetic trees for both taxa (for detailed methods see Appendix S1). True bugs sequences were aligned using MAFFT (Katoh et al. 2002; Katoh et al. 2005) and applying the G-INS-i algorithm for 18S, and FFT-NS-i algorithm for CO1 sequences. We used *Philaenus spumarius* (Cicadomorpha: Aphrophoridae) as outgroup. We generated a Bayesian chronogram using BEAST 1.8.1 (Drummond et al. 2012), within the CIPRES Science Gateway (Miller et al. 2010). We defined two partitions and applied the HKY+G substitution model for the 18S partition and GTR+G substitution model for the COI partition. Butterfly sequences were aligned using BioEdit (Tom Hall, Ibis Therapeutics, Carlsbad, CA, USA) and MAFFT (Katoh et al. 2002; Katoh et al. 2005). A Bayesian chronogram was constructed in BEAST 1.6.1 (Drummond et al. 2012). For detailed information on the reconstruction method see (Pellissier et al. 2013a). These trees (Appendix S2, S3) were used to calculate phylogenetic diversity metrics (see below).

For the Heteroptera, we pooled the species samples across years for each site to achieve a more complete species inventory. Indeed, because insect populations can fluctuate drastically between years, observations across several years provide more reliable data on species occurrences and abundances. Seventeen plots could not be sampled each year due to aggressive livestock grazing during the sampling period. Each plot was sampled at least six times (3 years x 2 months; one plot 4 times), but not necessarily every year. Even when pooling data, some plots still harbor a low species number (< 5 species), considering or excluding these plots from our analyses did not change the main results and thus we present data for the complete set of 150 plots. Butterfly data were available for one year and 137 plots. We removed three sites because species richness was one. Additional analyses excluding sites with less than six species did not change the results.

INSECT HERBIVORE PHYLOGENETIC DIVERSITY

The full phylogenetic trees were pruned to match the species pools of each region. These regional trees were used for calculations of phylogenetic diversity. We used two metrics of phylogenetic diversity, the mean pairwise distance (MPD) and the mean nearest taxon distance (MNTD). These metrics measure the phylogenetic distance at different depths of the phylogeny, with MPD accounting also for the basal nodes and MNTD focusing on the phylogenetic diversity at terminal parts of the phylogeny (Webb et al. 2002b). Along with this, we also calculated presence/absence and abundance weighted phylogenetic diversity for both insect groups. As with plant phylogenetic diversity, we decided to present the presence/absence based results (for abundance based results see Appendix S4). We calculated standardized effect sizes ((observed metric - expected metric) / standard deviation of expected metric)) for the phylogenetic diversity indices to test whether the phylogenetic community structure differs from random expectations. In addition, standardized effect sizes of phylogenetic diversity are less related to species richness. We used a null model that shuffles the tip labels of the phylogeny maintaining all other properties of the sample matrix (i.e. species richness in plots and species prevalence).

STATISTICAL ANALYZES

To test whether diversity of true bugs and butterflies increased along with plant diversity (species richness and phylogenetic diversity) and decreased with increasing LUI we used a set of explanatory variables. Region, plant species richness, plant phylogenetic diversity and LUI were included into a linear model. We further included the interactions between LUI and plant diversity measures into the model for butterfly species richness. In all other models there were no significant interactions between LUI and plant diversity measures. All

Table.1 Summary of linear models. Effects of region, plant species richness, plant phylogenetic diversity (standardized effect size), LUI (and its interactions with plant diversity) on true bug and butterfly species richness. ANOVA tables with bold numbers indicating significant effects. Missing values indicate that the explanatory variable was not included in the model.

	TRUE BUGS					BUTTERFLIES				
	Df	**SS**	**MSS**	**F**	***p***	**Df**	**SS**	**MSS**	**F**	***p***
Region	2	154.12	77.06	4.47	**0.013**	2	176.14	88.07	12.67	**<0.0001**
Plant SR	1	611.49	611.49	35.50	**<0.0001**	1	449.71	449.71	64.72	**<0.0001**
Plant SES MPD	1	0.36	0.36	0.02	0.89	1	24.43	24.43	3.52	*0.063*
Plant SES MNTD	1	79.85	79.85	4.64	**0.033**	1	10.47	10.47	1.51	0.22
LUI	1	8.29	8.29	0.48	0.49	1	28.32	28.32	4.08	**0.046**
LUI x Plants SR						1	39.23	39.23	5.65	**0.019**
LUI x Plants SES MPD						1	24.61	24.61	3.54	*0.062*
LUI x Plants SES MNTD						1	2.75	2.75	0.40	0.53
Residuals	143	2463.39	17.23			124	861.63	6.95		

Table 2 Summary of linear models. Effects of region, plant diversity (species richness and phylogenetic diversity) and LUI on the phylogenetic diversity (MPD and MNTD) of true bugs and butterflies in the three regions in Germany. ANOVA tables with bold numbers indicating significant effects.

	MPD						MNTD				
Heteroptera											
	Df	**SS**	**MSS**	**F**	***p***		**Df**	**SS**	**MSS**	**F**	***p***
Region	2	45.38	22.69	7.41	**0.0009**	Region	2	5.92	2.96	3.71	**0.027**
Plant SR	1	16.19	16.19	5.29	**0.0229**	Plant SR	1	6.89	6.89	8.64	**0.004**
Plant SES MPD	1	4.51	4.51	1.47	0.23	Plant SES MNTD	1	1.82	1.82	2.28	0.13
LUI	1	0.37	0.37	0.12	0.73	LUI	1	1.18	1.18	1.48	0.23
Residuals	144	440.85	3.06			Residuals	144	114.82	0.80		
Lepidoptera											
	Df	**SS**	**MSS**	**F**	***p***		**Df**	**SS**	**MSS**	**F**	***p***
Region	2	3.40	1.70	2.19	0.12	Region	2	0.79	0.39	0.40	0.67
Plant SR	1	0.25	0.25	0.33	0.57	Plant SR	1	0.15	0.14	0.15	0.70
Plant SES MPD	1	0.09	0.09	0.11	0.74	Plant SES MNTD	1	1.61	1.61	1.65	0.20
LUI	1	0.18	0.18	0.24	0.63	LUI	1	1.27	1.27	1.30	0.26
Residuals	128	99.43	0.78			Residuals	128	125.32	0.98		

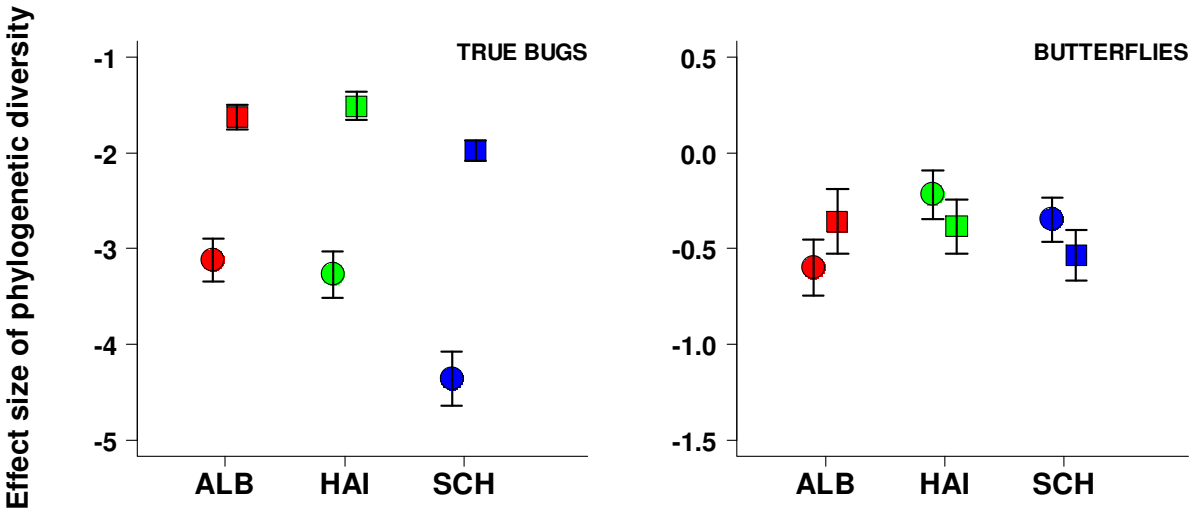

Figure 1 Mean (+- SE) phylogenetic diversity (standardized effect size of MPD and MNTD, values <-1.96 significantly different from 0) of herbivore assemblages in the three study regions. Colors indicate regions; ALB: Schwäbische Alb; HAI: Hainich-Dün; SCH: Schorfheide-Chorin, circles: MPD, squares: MNTD.

analyses were done using R version 3.0.3 (R Core Team 2014) and the adjusted package *picante* (Kembel et al. 2010).

Results

We sampled 133 true bug species and 58 butterfly species (see Appendix S4). True bug and butterfly species richness differed between regions (Fig. 1) and were strongly and positively correlated with plant species richness (Tab. 1). Further, true bugs species richness decreased with increasing plant MNTD (Tab. 1). Butterfly species richness was not affected by plant phylogenetic diversity, however there was a trend to increasing species richness with increasing plant MPD (marginally significant, Tab. 1). After accounting for the effects of region and plant diversity, butterfly species richness decreased with increasing LUI. For true bug species richness, LUI had no main effect after accounting for the variation explained by plant diversity. A significant interaction between LUI and plant species richness indicated that increasing land-use intensity altered the positive relationship between plant and butterfly species richness (Tab.1), i.e. the positive effect of plant species richness on butterfly species richness was weaker when land-use intensity was higher.

We found that plant species richness was positively correlated with true bug phylogenetic diversity, but not with butterfly phylogenetic diversity (Tab.2). We did not find any correlation between plant and true bug or butterfly phylogenetic diversities. Land-use intensification did not affect phylogenetic diversity of any of the two groups (Tab.2).

Discussion

Our results reveal positive relationships between plant and insect herbivore species richness and are therefore in line with recent findings (Manning et al. 2014). We found contrasting results when analyzing the relationship between plant species richness and insect herbivore phylogenetic diversity in the two groups. While true bug phylogenetic diversity was positively correlated with plant species richness, no such relationship was found with butterfly assemblages. Contrasting to our expectations, phylogenetic diversity of plant communities did not increase phylogenetic diversity in both, true bug and butterfly communities. In the same sense, land-use intensification had no effect on insect herbivore phylogenetic diversity.

Plant species richness vs. plant phylogenetic diversity as predictors of herbivore species richness

Experimental and non-experimental studies have shown that species richness of phytophagous insects increases with plant species richness (Scherber et al. 2010a; Dinnage et al. 2012; Pellissier et al. 2013b). In line with these studies we found an increase in

species richness of true bugs and butterflies with increasing plant species richness across virtually all regions (except for butterflies in Schorfheide). The ecological explanation of such a result is that high plant species richness increases resources and structural and temporal niches available for herbivores, which in turn leads to an increase in the number of consumers through niche differentiation (Brändle et al. 2001; Cardinale et al. 2006; Manning et al. 2014).

Contrary to our expectations and to the results of a recent study along an experimental plant diversity gradient (Dinnage et al. 2012), insect species richness showed no positive correlations with plant phylogenetic diversity. This supports findings of a non-experimental study on the relationship between plant diversity, climate and butterfly diversity by Pellissier et al. (Pellissier et al. 2013b) in the Swiss Alps. It seems that experimental studies might provide insight into mechanics behind plant – herbivore diversity relationships, but do not reflect more complex real world conditions. Thus, observational studies in non-experimental conditions seem to be more suitable in ecological studies that deal with the effects of trophic interactions on ecosystem functioning or processes. Interestingly, true bug species richness declined with increasing plant MNTD. Plant MNTD had a weak but significant effect on true bug species richness even after accounting for the effect of plant species

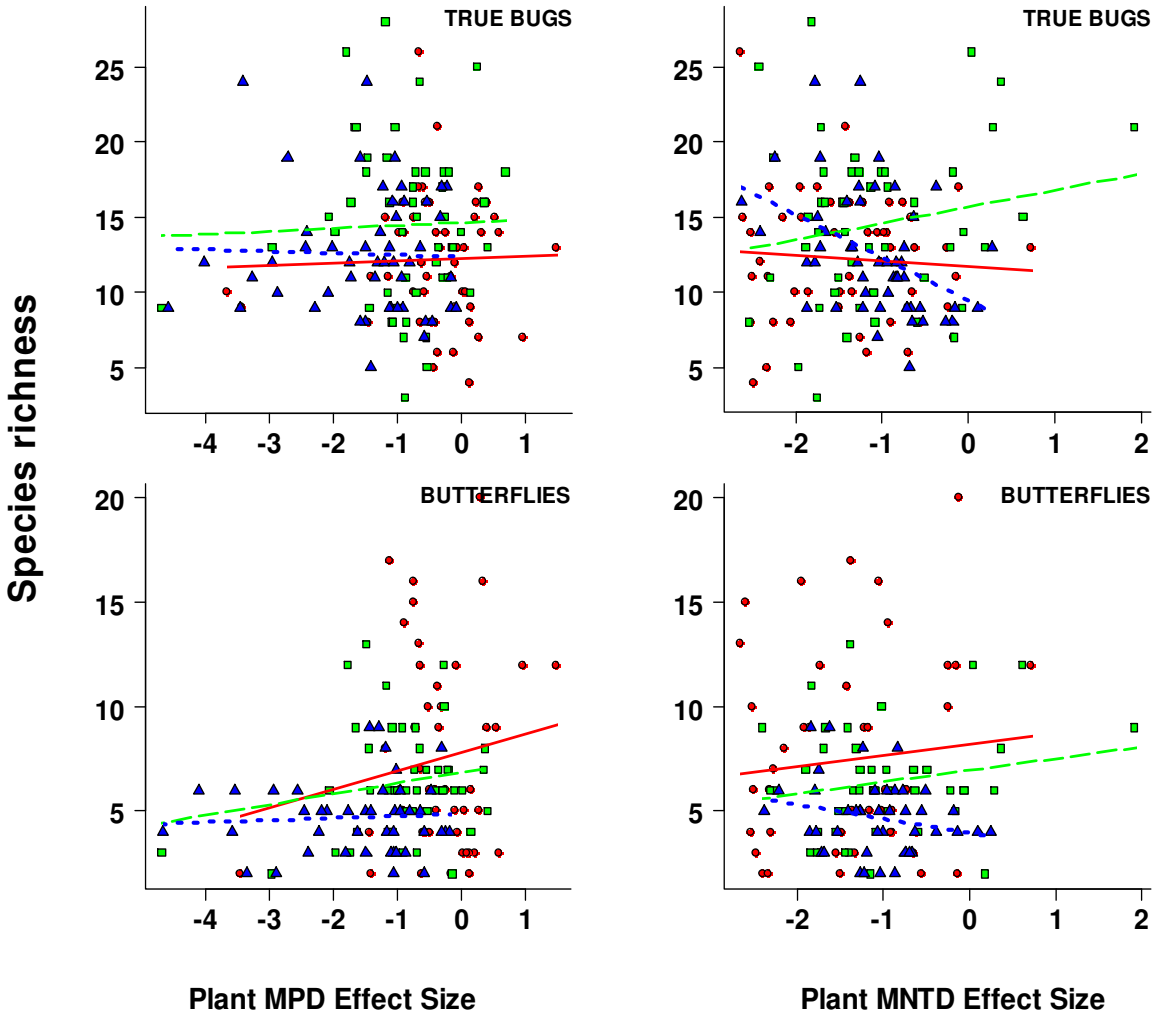

Figure 2 Relationships between true bug and butterfly species richness and plant phylogenetic diversity (standardized effect size of MPD and MNTD). Regression lines of different color indicate regions; red: Alb, green: Hainich, blue: Schorfheide

richness, thus indicating an effect independent of species richness. This is contrary to our expectations that plant phylogenetic diversity increases insect herbivore species richness. One may suggest that while plant communities contain more distantly related species at the tips of the phylogenetic tree (i.e. increasing MNTD), true bug species specialized on certain plant clades (i.e. family or genera) find less host plants. Thus, a decrease in true bug species richness with increasing nearest neighbor distance in plant communities could be caused by a decline in specialist true bug species. Therefore we suggest that the degree of specialization is an important key for the structure of the relationship between herbivore and plant communities (Castagneyrol et al. 2014). Future studies that incorporate feeding specialization and phylogenetic information could provide additional insights into this relationship and, for example, show whether plant phylogenetic diversity has different effects on specialist and generalist insect herbivores.

ARE THE PHYLOGENETIC DIVERSITIES OF INSECTS AND PLANTS WITHIN A COMMUNITY CORRELATED?

We found no relationships between plant and insect herbivore phylogenetic diversities. Our results suggest that measures of plant phylogenetic diversity at the alpha level might not provide reliable information about the functional space available for herbivores in natural communities. This can be explained by different mechanisms. First, some plant lineages might be colonized more often by herbivorous insects than others and some lineages may not be exploited at all (Pellissier et al. 2013b). These latter lineages might lead to an overestimation of available niches, a hypothesis supported by an effect of plant phylogenetic diversity on insect species diversity when only plants known to interact with butterflies are considered in the study of Pellissier et al. (Pellissier et al. 2013b). Thus, the importance of plant lineages in structuring herbivore communities may vary according to the specificity in host-use. Second, it is also possible that functional traits of plants and insects important for structuring trophic interactions are not conserved. Third, since phylogenetic diversity conflates several evolutionary and ecological processes (e.g. coevolution, selection), interpreting the ecological meaning and consequences of gains and losses of phylogenetic diversity is not straight-forward in the absence of trait information. However, the link between traits and ecological functions is well understood in plants but less in animals (de Bello et al. 2010)**.** In general, morphological traits (e.g. body size) in animals are strongly conserved (Harmon et al. 2010), whereas ecological traits such as niche-breadth, which are particularly important for the interaction of species with other species and the environment, seem to be more labile (Blomberg et al. 2003). A preliminary analysis of our dataset shows a positive correlative trend between herbivore phylogenetic diversity and community weighted means of plant traits with low phylogenetic signal (Appendix S5 in Egorov et al. 2014). Based on this, it seems that in our study the decrease in plant phylogenetic diversity is less likely to affect the functional niches of herbivores, and thus does not decrease herbivore species richness or phylogenetic diversity.

THE EFFECT OF LAND-USE ON INSECT DIVERSITY

Prior to the phylogenetic diversity, LUI had a strong negative effect on butterfly species richness, what agrees with previous studies (Börschig et al. 2013). It is important to note that in our case, the effect of LUI remained strong even after accounting for region, plant species richness and phylogenetic diversity. This emphasizes the importance of considering factors other than species richness (*e.g.,* land use) when attempting to evaluate the effects of disturbance and trophic interactions on diversity of consumers. However, for true bug species richness, LUI did not explain any variation in species richness after accounting for the plant diversity effects. When LUI was set prior to plant diversity in the sequentional ANOVA, the negative effect of LUI was significant. This indicates that depending on the insect group, LUI can have direct or plant diversity mediated effects on the herbivore species richness. To gain insight on the mechanics behind these patterns, more studies are needed that include more and different insect herbivore groups. For instance the developmental biology of the insect groups might play a role (hemimetabolous vs. holometabolous) or the diet changes between juvenile and adult stages.

We could not find any support for a negative effect

of land-use on herbivore phylogenetic diversity. Two mechanisms might explain this lack of relationships. First, traits enabling herbivores to cope with high land-use intensities might be not phylogenetically conserved, thus leading to a random loss of species. Identifying which herbivore traits might be crucial for species assembly in differently used grasslands is, however, still limited (but see (Börschig et al. 2013). Second, the effect of land use on phylogenetic community structure of herbivores might be diluted by other environmental factors (e.g. temperature, exposure, soil conditions). However, to test the importance of such causal relationships would require experimental approaches that were not applied in this study.

Overall, our analyses did not reveal any strong and consistent relationship between phylogenetic diversity of plants, land-use intensity and diversity of two groups of primary consumers. This might be due to the overestimation of potential niches for herbivores, as not all plant lineages contribute to the structuring of consumer communities (Pellissier et al. 2013b). This calls for the implementation of plant – herbivore networks into phylogenetic analyzes, which would provide deeper insights into trophic interactions and consequently their effects on ecosystems. Another approach to analyze phylogenetic diversity in trophic interactions could include analyzing beta diversity, an approach that will be handled in another study. Based on recent results, phylogenetic turnover of plants seems to be a strong predictor of herbivore beta diversity (Pellissier et al. 2013b). To generalize the effects of plant diversity on herbivore assemblages it might also be useful to combine phylogenetic diversity of different herbivore taxonomic groups to a measure of phylogenetic "multidiversity" similar to taxonomic "multidiversity" (Allan et al. 2014). Different clades of herbivorous insects as well as herbivorous guilds prefer different clades of plant hosts and show phylogenetic patterns in host use (Weiblen et al. 2006; Novotny et al. 2010). Thus, analyzes of trophic interactions covering only a few groups of herbivorous insects may not represent the conditions of the whole herbivore community. General bottom-up effects in trophic interactions might be revealed using a supertree approach to calculate phylogenetic diversity of all herbivorous insect taxa.

Chapter 4

PLANT PHYLOGENETIC DIVERSITY INCREASES INVERTEBRATE HERBIVORY IN MANAGED GRASSLANDS.

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Manuscript in preparation

ABSTRACT

Plant diversity and land-use intensity are suggested to be important drivers of invertebrate herbivory. The strength and direction of the reported relationships however varies greatly. Recently it has been proposed that considering the phylogenetic structure of plant communities may improve our understanding of the mechanics behind the diversity – herbivory relationships. Here, we hypothesized that plant phylogenetic diversity is a stronger predictor of invertebrate herbivory than plant species richness or single functional diversity measures. Further we hypothesized that land-use effects on herbivory are mediated by plant phylogenetic diversity. We assessed invertebrate herbivory and plant diversity across a range of land-use intensities including a total of 145 managed grasslands in three regions in Germany. Land use affected plant species richness and phylogenetic diversity negatively. We found that plant species richness was only a poor predictor of herbivory. By contrast, plant phylogenetic diversity had a strong positive effect on herbivory even after accounting for the effects of region and land use. The strength of direct and indirect effects of land use and phylogenetic diversity varied among regions. Our results suggest that increasing phylogenetic diversity of plant communities increases invertebrate herbivory probably by providing more food resources. Differences between regions suggest to account for regional peculiarities when attempting to generalize land-use effects on invertebrate herbivory.

INTRODUCTION

Plant diversity and land-use intensity has been shown to be important predictors of invertebrate herbivory (e.g. Scherber et al. 2006; Scherber et al. 2010b; Gossner et al. 2014). Previous studies that focused on responses of herbivory to changes in plant species richness revealed, however, no consistent patterns. There is an approximately equal number of studies found either positive or negative relationships between herbivory and plant species richness (reviewed in Dinnage 2013). Several studies including additional predictors also found no relationships between plant species richness and herbivory, thus, stating that plant species richness was not the major determinant of herbivory response (Scherber et al. 2006; Scherber et al. 2010b). Species richness is, however, only a rough and very simple descriptor for diversity within ecological communities. By contrast, community phylogenetics integrate information on different plant traits, which are may be related to herbivory but often are difficult to assess (for instance biochemical or mechanical defense mechanisms) into a phylogenetic diversity index. This may provide a more comprehensive picture on the effects of plant diversity on herbivory when compared with conventional species richness or functional estimates. Several studies already used community phylogenetics in addition to species richness and showed that phylogenetic diversity of plant communities had strong and often independent effects on herbivory. The studies used, however, two approaches to assess herbivory. First, herbivory was measured on one ("focal") plant species in monocultures/low diversity plots and within high diversity plots. Second, herbivory measured at community level, where herbivory on all plant species was assessed. In a recent meta analysis, using the first approach, Castagneyrol et al. (2014) showed that herbivory in mixed and pure forests depended on both, herbivore specialization and plant phylogenetic diversity. While specialist herbivores damage or abundance was related only to the abundance of their focal host plants, generalist herbivory decreased in mixed forests, but only with increasing phylogenetic distance between host trees and associated trees. Using the second approach, Dinnage (Dinnage 2013) showed that although plant phylogenetic diversity had only a marginally significant negative effect on herbivory, there was a significant interaction between plant species richness and phylogenetic diversity. Plant species richness had a positive effect on invertebrate herbivory, but this effect was altered by the phylogenetic diversity of plant assemblages, i.e. the positive effect of species richness on herbivory decreased with increasing plant phylogenetic diversity. Parker et al.

(Parker et al. 2012) found a contrasting pattern where increasing phylogenetic distance between plants increased the impact of herbivores. The authors explained this pattern with increasing generalist herbivores damage. Although plant phylogenetic diversity seems to be good predictor of herbivory, the opposing results indicate that the strength and direction of the effect depends on the system studied and consequently on the plant and the herbivore community composition (e.g. functional composition of plant communities, specialist-generalist ratio, feeding guilds). In addition, herbivory measured at species level is expected to decrease when more and distantly related species are present in the community, due to shift of mostly generalist herbivores to another plant species. In contrast, we expect an increase in overall herbivory damage with increasing plant phylogenetic diversity, due to provision of additional feeding niches to a greater number of herbivores. While both, species specific and community level herbivory contribute to our understanding of the herbivory-plant phylogenetic diversity relationships, for ecosystem functions, changes on community level are more important than single interactions. In addition to biotic interactions, anthropogenic pressure (i.e. land-use intensification) can also affect invertebrate herbivory. Gossner et al. (Gossner et al. 2014) showed that invertebrate herbivory in temperate managed grasslands decrease with increasing land-use intensities. The authors hypothesized that several direct and indirect effects of increased land-use intensity might cause the strong herbivory decline, e.g. direct effects of mowing on generalist herbivores or indirect effects via reduced plant species richness and increased proportion of grasses. Land-use intensification has been shown to decrease phylogenetic diversity of communities (Dinnage 2009; Egorov et al. 2014) and thus, an indirect effect of land use might also be caused by changes in community phylogenetics. Although several studies showed that plant diversity and anthropogenic influence affected herbivory separately, studies that incorporate both in one analysis are still scarce.

In this study we focus on invertebrate herbivory in temperate managed grasslands. We aim at analyzing the relationships between land use, plant diversity, and herbivory by using a comprehensive dataset of 145 grassland plots in three regions in Germany We hypothesize that phylogenetic diversity is a better predictor of herbivory than species richness or individual functional diversity components (i.e. proportion of grasses). Thereby we assume that phylogenies contain more information on community structure and phenotypic and functional composition of plants, that are important determinants of invertebrate herbivory, than species richness (Scherber et al. 2010b; Parker et al. 2012; Dinnage 2013). Since associational resistance to generalists seems to be found more often in studies that focus on species-specific herbivory, we expect to find a positive relationship between herbivory and plant phylogenetic diversity on community scale due to provision of additional feeding resources to a greater number of invertebrate herbivores.

In addition to biotic interactions, land use has been shown to cause direct negative effects on herbivory (Gossner et al. 2014), as well as on plant species richness (Socher et al. 2013) and phylogenetic diversity (Egorov et al. 2014). We hypothesize that indirect effects of land use on herbivory via changes in plant communities are more important than direct effects. In particular we predict that indirect land use effects are mediated by changes in phylogenetic diversity of plant communities rather than species richness or proportion of grasses.

METHODS

STUDY REGION

Our study was conducted within the Biodiversity Exploratories (www.biodiversity-exploratories.de), a large-scale and long-term project on the relationships between land-use intensity, biodiversity and ecosystem functioning. The Biodiversity Exploratories consist of three regions in Germany (Schwäbische Alb; 460–860 m a.s.l., 48°43′ N 9°37′ E; Hainich-Dün: 285–550 m a.s.l., 51°20′ N 10°41′ E; and Schorfheide Chorin: 3–140 m a.s.l., 53°02′ N 13°83′ E) covering a south-west – north-east gradient. Each region comprises 50 grassland and 50 forest plots under different land-use types and intensities. For more details see Fischer et al. (Fischer et al. 2010). Our study focused on the grassland plots for a total of 145 plots in the three regions.

LAND USE

Land-use information of the study plots was obtained by yearly interviews with farmers and land-owners between 2006 and 2010. Due to variability in land-use intensity between years (Blüthgen et al. 2012), we used the mean between all years to better cover the long-term management. Information on three types of land use was acquired; fertilization (kg nitrogen ha−1 year−1), mowing frequency (number of cuts year−1), and grazing intensity (livestock units×days of grazing ha−1 year−1). The land-use types were standardized and summed up to a combined quantitative land-use intensity index (LUI; Blüthgen et al. 2012). The yearly LUI-values were averaged for each of the 145 plots for the five-year period and the obtained means were used for our analyses.

PLANT SPECIES RICHNESS, FUNCTIONAL COMPOSITION AND PHYLOGENETIC DIVERSITY

Between 2009 and 2011 vegetation on a 4 m×4 m plot in each of the 145 grasslands was measured yearly. For each plot, vascular species richness and their relative abundance in percent cover was estimated. Based on these data we calculated the species richness as the average richness per plot across the three years. In addition, the proportion of grasses was estimated as the proportion of total biomass (Gossner et al. 2014) in all samples of the herbivory assessment (see below).

Phylogenetic relatedness of species was obtained from a well resolved and dated phylogeny of the Central European flora (Durka and Michalski 2012). In brief, this phylogeny was assembled by manually grafting subtrees on a backbone topology, dating of nodes based on fossil records using the bladj algorithm in PHYLOCOM (Webb et al. 2008) and calculating an ultrametric tree (for details see Durka and Michalski 2012). We pruned the overall phylogeny to match the species pool of each of the three regions. As a result we obtained three trees, one for each region, representing the phylogenetic relationships of the respective species pool.

Phylogenetic diversity of plant species was calculated with the "picante" package in R (Kembel et al. 2010). For each plot and year, we calculated the mean pairwise distance (MPD) (Webb et al. 2002b). We then calculated averages across the three years and used the mean MPD for each plot for further analyses (Egorov et al. 2014). Phylogenetic diversity was calculated using presence/absence and abundance weighted data (% cover). In general, results based on presence/absence and abundance data did not differ strongly and since abundance of (potential host) plants plays a major role in herbivore – plant diversity relationships (Root 1973; Solomon 1981; Otway et al. 2005) we focus here on results based on abundance data.

HERBIVORY

Herbivory was measured in all plots in May 2013 before mowing took place. To prevent livestock grazing temporary electrical fences were installed in early spring. Five plots had to be excluded from analysis since grazing by cattle in the fenced patches was likely, resulting in a total of 145 analyzed plots. In each patch two random sampling points were chosen and from each sampling point 100 leaves were collected randomly from grasses and forbs relative to their estimated proportion of biomass in the sample. Damaged leaf area was measured by eye using templates ranging from 1 mm^2 and 500 mm^2. Four different damage types were considered (chewing, sap sucking, leaf mining and rasping), but only the total leaf damage was noted. Proportion of leaf area damaged was calculated by dividing damaged area by the sum of leaf area measured using a LI-COR area meter (LI-3000C, Lincoln (NE) USA) and the damaged area. Herbivory values were log transformed to approximate normality. For further details see Gossner et al. (Gossner et al. 2014).

STATISTICAL ANALYSES

We first used univariate analyses to test for the effects of plant diversity on herbivory. The initial model included region, LUI, proportional biomass of grasses, plant species richness, plant phylogenetic diversity, interactions between region and all other variables, interactions between LUI and plant diversity (species richness and phylogenetic diversity) as well as proportion of grasses and interaction between plant species richness and plant phylogenetic diversity. We then applied the stepAIC algorithm (direction criterion = "backward") in the R package MASS (Venables and Ripley 2002) to

simplify the model based on the Akaike Information Criterion and selected the model with the lowest AIC value. To test for the effect of plant diversity independent of land-use intensity and proportion of grasses we used sequentional ANOVAs with region, LUI and grass proportion being the first variables entered in the model. Plant diversity metrics (species richness and phylogenetic diversity) were fitted at last to explain additional variation.

We further used structural equation modeling with the package "lavaan" (Rosseel 2012) to test for direct effects of land use on herbivory and indirect effects of land use, mediated by proportion of grasses, plant species richness and plant phylogenetic diversity. In the model we defined herbivory, proportion of grasses and plant diversity (species richness and phylogenetic diversity) as being affected by land use (one-way arrows in the diagram). We further stated that herbivory is affected by plant species richness and plant phylogenetic diversity as well as proportion of grasses. Since higher proportion of grasses can decrease the mean phylogenetic distance between species in assemblages we also defined that plant phylogenetic diversity is affected by the proportion of grasses. And finally we assumed that plant species richness and plant phylogenetic diversity correlate with each other (two-way arrows in the diagram). Based on the χ^2 statistic, the model for Schorfheide provided a bad fit and did not converge well. We therefore excluded the variable the least significance values (highest *p*-values) form the model, which resulted in a much better fit of the data. All analyses were conducted in R 3.0.3 (R Core Team 2014).

RESULTS

Mean number of plant species per plot in the three years was 26.9 (min: 13.3; max: 55.6). Mean phylogenetic diversity (mean pairwise distance in million years) was 192.1 (min: 55.9; max: 242.2). Average herbivory in the three regions was 1.05% (min: 0.05%; max: 5.6%). Herbivory rates differed between regions ($F_{2,142}$=9.78, p<0.001) with highest mean rates observed in Schorfheide (1.26%) followed by Alb (1.22%) and Hainich (0.68%). Increasing LUI and proportion of grasses decreased herbivory in all three regions ($F_{1,139}$=20.6, p<0.001 and $F_{1,139}$=6.1, p=0.015, respectively). Plant species richness had no significant effect on herbivory and was removed as a predictor in the model with abundance based phylogenetic diversity (Tab.1). Phylogenetic diversity had a strong positive effect on herbivory (Fig.1) even after accounting for the effects of region, LUI and proportion of grasses (Tab.1).

According to the goodness of fit measures the model for Schorfheide provided the best fit to the data, whereas the model for all three regions combined provided the least close fit (Tab.2). No correlation between the variables in our models was significant in all four models, indicating that the strength of the relationships differed between regions (Fig.2). Land-use intensity negatively affected plant species

Table 1 Linear model summary. Effects of region, LUI, proportion of grasses, plant species richness and plant phylogenetic diversity on herbivory in the three regions. ANOVA tables of the best fit model with lowest AIC score (R^2=0.41). Bold numbers indicate significant effects.

	Df	SS	MSS	F	*p*
Region	2	12.53	6.26	20.19	**<0.0001**
LUI	1	7.50	7.50	24.18	**<0.0001**
Proportion Grass	1	3.77	3.77	12.15	**0.00066**
PD	1	2.74	2.74	8.82	**0.0035**
Region x PD	2	1.20	0.60	1.93	0.15
LUI x Proportion Grass	1	1.00	1.00	3.23	*0.074*
Residuals	136	42.20	0.31		

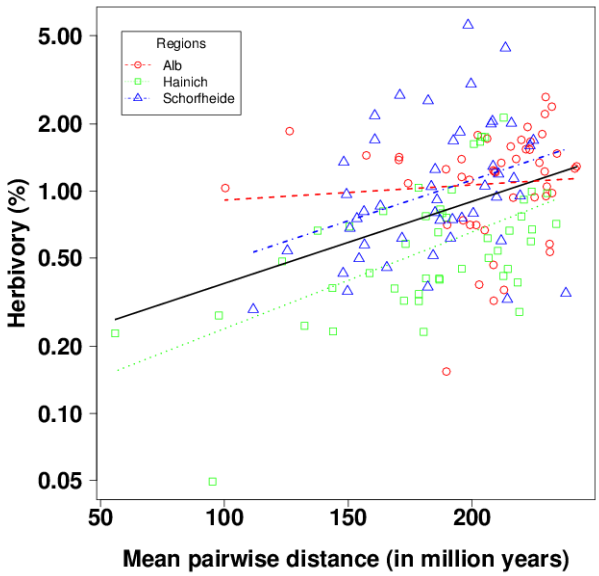


Figure 1 Relationships between herbivory (measured as percentage of leaf area damaged) and phylogenetic diversity of plant communities (MPD) in the three regions in Germany (n=145). Solid line fitted over the three regions combined.

Table 3 Direct, indirect and total effects of LUI on invertebrate herbivory in 145 grassland plots in three regions in Germany.

	ALL	ALB	HAINICH	SCHORFHEIDE
Direct	-0.34	-0.19	-0.15	-0.31
Indirect	-0.04	-0.1	-0.42	-0.05
Total	-0.38	-0.29	-0.57	-0.36

richness (except Schorfheide-model) and plant phylogenetic diversity (except Alb-model). Proportion of grasses was not affected by land use in Hainich, Schorfheide and in all three regions combined, whereas in the Alb, land use had a negative effect on the proportion of grasses (Fig.2). A direct negative effect of LUI on herbivory was found in Schorfheide and across the three regions combined. Indirect negative effects of LUI on herbivory were mediated by changes in the plant community mainly in Hainich and Alb. In Alb the direct and indirect negative effects of LUI were roughly equal, while in Hainich the direct effect was weak whereas the indirect effects were high (Tab.3, Fig.2).

DISCUSSION

We showed that plant phylogenetic diversity is a strong predictor of invertebrate herbivory in temperate managed grasslands. Contrary to plant species richness it significantly explained variance in herbivory even after accounting for the effects of land-use intensity. Higher phylogenetic diversity increased invertebrate herbivory, a result opposed to those of previous studies but in line with our hypothesis. Land use had an overall direct negative effect on herbivory and indirect effects were mediated by changes in plant phylogenetic diversity rather than plant species richness. But note that most of the analyzed relationships differed in their strength among regions suggesting additional, region specific processes.

EFFECTS OF PLANT DIVERSITY ON INVERTEBRATE HERBIVORY

Our results are in accordance with previous studies that showed the poor predictive power of plant species richness on invertebrate herbivory (Hanley 2004; Scherber et al. 2010b). However, several other studies that found either a negative or a positive effect of plant species richness (reviewed in (Dinnage 2013)) indicating that the role of plant species richness varies in context of plant and herbivore community composition. We therefore suggest that more studies across different habitat types are needed to disentangle the importance of plant diversity and community composition on herbivory. Note also that there are two approaches to study herbivory responses. First, the community-wide herbivory can be measured including herbivory damage on all plant species. Second, plant-specific herbivory can be measured, where certain plant species serve as "phytometers" and the herbivory damage is assessed on these plants only (Gibson 2002). Thus, results between studies using different approaches might not be easy comparable. It is important to note that in our study no plant-species specific herbivory data were available and herbivory damage was assessed community-wide. Finally, Dinnage (Dinnage 2013) found a negative relationship between plant phylogenetic diversity and herbivory (although not significant) in grasslands. There was also an interaction between species richness and phylogenetic diversity, indicating that increasing phylogenetic diversity weakens the positive effect of plant species richness on herbivory (Dinnage 2013). This is contrasting to our results probably due to the setup of the study. While Dinnage (Dinnage 2013) used certain species as "phytometers" (Gibson 2002; Scherber et al. 2006) we conducted our analysis on the community level. Therefore direct comparisons are difficult (see above). In addition, Dinnage (Dinnage 2013) analyzed herbivory on forbs only, excluding grasses from the analysis. In our study the proportion of grasses had a strong negative effect on plant phylogenetic diversity, and thus should alter the effect of plant phylogenetic diversity on herbivory.

Table2 Goodness of fit measures from the output of the four structural equation models of the correlations between land-use intensity, plant diversity and herbivory in the 145 grassland plots in three regions in Germany. GFI: Goodness-of-fit; RMSEA: root mean square error of approximation.

	$\chi 2$	df	*p*	GFI	RMSEA
ALB	0.001	1	0.977	1	0
HAINICH	0.08	1	0.777	0.999	0
SCHORFHEIDE	0	0	1	1	0
ALL REGIONS	2.421	1	0.12	0.993	0.099

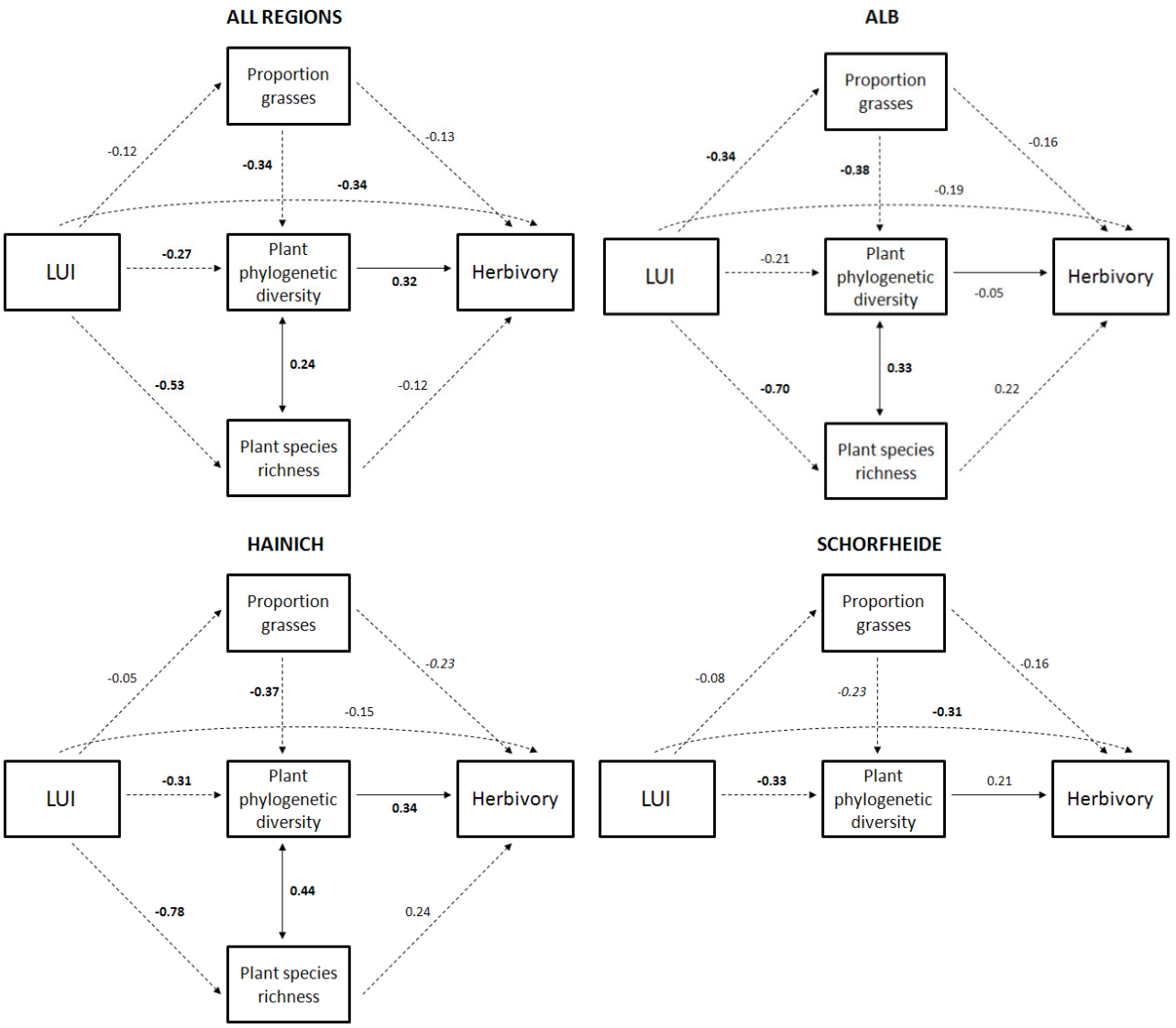


Figure 2 Structural equation models of the relationships between land-use intensity (LUI), plant diversity (proportion of grasses, plant species richness, plant phylogenetic diversity) and herbivory in the three regions separately and combined. Path lines: dashed lines: negative path coefficients, solid lines: positive path coefficients. Bold numbers indicate significant path coefficients.

On the other hand, in a meta-analysis Parker et al. (Parker et al. 2012) found an increase in herbivore impact with increasing phylogenetic distance on community level which oppose the results by Dinnage (Dinnage 2013). Parker et al. (Parker et al. 2012) analyzed studies from a range of different biomes, including terrestrial (grasslands, forests, deserts) as well as aquatic (marshes and lake bottoms) systems. Thus, the results of Parker et al. (Parker et al. 2012) might be more comprehensive and reveal more general patterns. Stronger impact of herbivores with increasing phylogenetic diversity of plant communities was explained by a higher pressure from generalist herbivores. This might be caused by either generalists being able to feed on a wide range of distantly related plant clades or feeding on the most abundant plants, which were distantly related in the analyzed studies (Parker et al. 2012).

Our results reveal similar effects of phylogenetic diversity on herbivory. Explaining the underlying mechanisms by means of the contribution of specialist vs. generalist herbivores to herbivory is with the data on our hand not possible, since we have no information on the proportion of herbivory damage done by specialist and generalist herbivores. Such differentiations are in "natural" grasslands in our opinion not feasible because of the high number of species of both plants and herbivores. Here experimental approaches with simplified artificial plant and herbivore community may be more helpful. Moreover, herbivory on community scale might express different patterns along plant diversity gradients compared to species-specific herbivory.

Since changes in ecosystems often happen on community scale, assessing herbivory on community scale might be the more appropriate approach in macroecological studies.

DIRECT VS. INDIRECT EFFECTS OF LAND-USE INTENSITY ON HERBIVORY

Although there were differences between regions, the relationships between several variables in some regions were strong enough to persist even when combining data from all regions. The direct effect of LUI on herbivory was larger than the indirect effects. This was also stated by Gossner et al. (Gossner et al. 2014) who hypothesized that mowing in particular decreases herbivory, although the indirect effects of land use were not explicitly tested for in this study. The structural equation model showed no significant indirect negative effect of land-use intensity on herbivory mediated by plant species richness or plant phylogenetic diversity when all three regions were analyzed together. However, this might be caused by opposing directions of the effects of LUI and phylogenetic diversity on herbivory. Nevertheless, LUI decreases the positive effect of phylogenetic diversity on herbivory by reducing phylogenetic diversity directly (Egorov et al. 2014) and indirectly through changes in plant species richness (Socher et al. 2012). As the models for each region showed, direct and indirect effects of land use vary between regions. Especially in Hainich land use decreased herbivory indirectly, this could be explained by particularly strong effect of land use on species richness and phylogenetic diversity (Egorov et al. 2014) compared to other regions. Regional peculiarities (e.g. soil type) can alter the effect of land use on plant diversity (Socher et al. 2012). Hence, while on a broad scale land-use intensification directly decreases invertebrate herbivory, this cannot be applied to communities on regional scale. This calls for caution when trying to apply general assumptions on smaller scales

CONCLUSION

We show that phylogenetic diversity of plants is a better predictor of invertebrate herbivory in managed grasslands than plant species richness. Community phylogenetics provides a useful framework when analyzing herbivory and may improve our understanding about the mechanisms causing different levels of herbivory. However, additional information on specialization of involved herbivores might help to resolve the underlying mechanisms. Therefore experiments are needed. We further show that in general land use has a direct effect on herbivory, but direction and strength of the effect varies among region. Thus, it is important to consider each region separately to fully resolve the relationships between land use, plant diversity and invertebrate herbivory. While land use seems not to have profound indirect effects on herbivory via changes in phylogenetic diversity, relative effects in relation to effects mediated through decrease in invertebrate diversity are still unclear. Thus incorporation of herbivore diversity and abundance may provide additional insights on the effect of land use on invertebrate herbivory.

Chapter 5

SUMMARY AND OUTLOOK

SUMMARY

In this thesis, I studied the effects of land-use intensification on phylogenetic diversity of plant and herbivorous insect communities, as well as on invertebrate herbivory in managed grasslands in three regions in Germany. Land-use intensification in general causes a decline in taxonomic diversity of plant and herbivorous insect communities in managed grasslands. It may also alter the phylogenetic structure of communities, leading to communities that contain species that are closer related than expected. In addition land use and land-use induced changes in plant diversity may also affect ecosystem functions and processes such as productivity or interactions with higher trophic levels.

In the first chapter, I present a general introduction and aims of my thesis. I briefly outline the current knowledge about the effects of land-use intensification on phylogenetic diversity in plant and animal communities and interactions between the latter. Further, I outline the relationships between plant diversity and invertebrate herbivory and put it in the context of land-use intensification.

In the second chapter, I studied how land-use intensification alters the phylogenetic composition of plant communities in managed grasslands. In particular, I tested whether land-use intensification leads to phylogenetic clustering. First I calculated phylogenetic diversity for all, common and rare species assemblages in the study plots. Then I used a null model to test whether communities contain more closely related species than expected with increasing land-use intensities. I found that phylogenetic diversity decreased only weakly with increasing land-use intensity. Moreover, there were no significant differences in the response of common and rare species assemblages to increasing land use. There were, however, regional differences in the strength and direction of several land use – phylogenetic diversity relationships. The results suggest that land use is not a major determinant of plant phylogenetic community structure in managed grasslands. One explanation might be that land use sensitive traits are not phylogenetically conserved. Further, combining different components of land use into one measure might neglect the effects of the different land-use types on the phylogenetic diversity of plant communities. Differences in the responses between regions also suggest to account for the regional peculiarities when analyzing the land use – phylogenetic diversity relationships. Phylogenetic diversity might nevertheless be used as a complement, rather than a proxy of other diversity metrics to assess the effects of anthropogenic disturbance on biological communities.

In the third chapter, I studied the relationships between land-use intensity, plant diversity and insect herbivore phylogenetic diversity. In particular, I tested whether phylogenetic diversity of plants is an additional predictor of insect herbivore diversity beyond plant species richness. I further tested whether plant and insect herbivore phylogenetic diversities are positively correlated. And last I tested whether land-use intensification decreases phylogenetic diversity in insect herbivore communities. First, I constructed molecular phylogenies of true bug and butterfly assemblages in the studied grassland plots. Then, I calculated phylogenetic diversity of the two herbivorous insect groups. I used a null model to calculate phylogenetic diversity independent of species richness and to test whether the communities' diversity differs from random expectations. Finally, I used linear models to test for the effects of land use and plant diversity on herbivore insect diversity in the three regions in Germany. Species richness of the two insect groups increased with increasing plant species richness while phylogenetic diversity of plants explained only little additional variance in insect species richness. Phylogenetic diversity of true bugs and butterflies showed no relationships with land use and plant phylogenetic diversity. The results indicate that land use might favor traits in herbivorous insects that show phylogenetic divergence or are randomly distributed along the phylogeny, causing a random loss of species. In addition, the evolutionary history of plant assemblages does not affect phylogenetic structure of herbivore insect communities. This might probably be caused by overestimating niche availability due to clustered specialization of insect herbivores. In conclusion, in managed grasslands land use and plant phylogenetic diversity do not predict phylogenetic diversity of herbivore

assemblages.

In the fourth chapter, I studied how plant species richness and phylogenetic diversity affect invertebrate herbivory. Further, I tested whether land use have direct or plant diversity mediated effects on herbivory. I used linear models to test whether plant diversity effects herbivory after accounting for the effects of land use. Then, I used structural equation modeling to test for direct and indirect effects of land use on invertebrate herbivory. Plant species richness was not related to herbivory, however, herbivory increased strongly with increasing phylogenetic diversity of plant communities. In general, land-use intensification had a strong direct negative effect on invertebrate herbivory rather than indirect effects *via* changes in plant diversity. However, this pattern differed strongly between regions with all possible combinations (i.e. weak direct and indirect effects in the first region, weak direct and strong indirect effects in the second region, and strong direct and no indirect effects in the third region). The results suggest that invertebrate herbivory is strongly affected by land-use intensification. Whether these effects are direct or plant diversity mediated depends, however, on regional idiosyncrasies. Thus, caution is needed when attempting to generalize herbivory response to land-use intensification. Further, plant phylogenetic diversity proved to be a better predictor than species richness or single functional diversity metrics, suggesting that evolutionary history of plant communities should be considered in further analyzes of plant diversity – invertebrate herbivory relationships.

OUTLOOK

This study has raised several questions about the importance of community phylogenetics in studies of the relationships between biodiversity, anthropogenic disturbance and ecosystem functioning. First, in managed grasslands land use is an overall weak predictor for plant and insect phylogenetic diversity, although species richness declines strongly along land-use gradients. Close relatives among plant and insect herbivore lineages seem to differ in the response to increasing land use creating a more or less idiosyncratic pattern along land-use gradients. Identification of potentially land-use sensitive traits (Pfestorf et al. 2013) and their comparison between species that are able to deal with high land-use intensities and species that cannot might be helpful to explain the weak correlation between phylogenetic diversity and land-use intensity. In this context, the phylogenetic signal of land-use sensitive traits is a crucial point in the understanding of land-use effects on phylogenetic diversity of plant and animal communities. Hence, assessment of functional traits related to land use, especially in insect herbivores (Börschig et al. 2013), and the amount of phylogenetic signal in them is needed to explain the mechanics behind the weak relationships between land use and phylogenetic diversity. Second, the study of the relationships between plant phylogenetic diversity and insect herbivore phylogenetic diversity was carried out on alpha scale. Phylogenetic turnover in plant communities may be a strong predictor of phylogenetic turnover of insect herbivore communities (Nipperess et al. 2012; Pellissier et al. 2013b). Further studies in this direction could reveal stronger bottom up control of consumer phylogenetic diversity through phylogenetic turnover of plant communities and associated traits. Third, I did not explicitly test for the phylogenetic association between plants and herbivores. If plant species or lineages that are not used as hosts by insect herbivores were removed from the dataset, such as only phylogenetic diversity of species known to interact with the herbivores would be considered, the relationship between plants and herbivore phylogenetic diversity may become stronger (Pellissier et al. 2013b). Due to a possible overestimation of available niches for herbivores, including all plant species and lineages might dilute the effects of plant phylogenetic diversity on consumer phylogenetic diversity. In the same sense, additional herbivore groups such as Coleoptera or Auchenorrhyncha could be included into analyzes to complement the insect herbivore assemblages. This can give a more comprehensive picture of the relationships between insect herbivore phylogenetic diversity and plant phylogenetic diversity than analyzing only subsets of the insect herbivore community. Fourth, despite the strong effects of plant phylogenetic diversity on herbivory, with the data available it is difficult to explain how exactly

plant evolutionary history affects invertebrate herbivory. It is important to know whether plant phylogenetic diversity affects specialist or generalist invertebrate herbivores (Castagneyrol et al. 2014) and to which degree the involved herbivores exhibit host specialization. Hence, in a next step the identification of the herbivore species should be considered as well as the identification of their host plans. The latter could be accomplished by literature review or feeding experiments. This additional information is mandatory to explain the mechanics behind the relationship between plant phylogenetic diversity and invertebrate herbivory.

DEUTSCHE ZUSAMMENFASSUNG

Intensivierung in der Landnutzung führt in terrestrischen Ökosystemen häufig zu einem Verlust von Biodiversität. Um die Auswirkungen dieser Verluste auf die Ökosysteme besser abschätzen zu können, benötigen wir ein genaueres Verständnis der Beziehungen zwischen Landnutzung, Biodiversität und Ökosystemfunktionen und –prozessen. Biodiversität umfasst neben Artenreichtum und funktioneller Diversität auch die evolutionären Beziehungen innerhalb von Artengemeinschaften, die sogenannte phylogenetische Diversität. Die phylogenetische Diversität von Artengemeinschaften wird häufig als gleichwertig oder als Ersatz für funktioneller Diversität betrachtet, hat aber gegenüber der funktionellen Diversität den Vorteil, dass *a priori* keine subjektive Auswahl von funktionell bedeutsamen Artmerkmalen gemacht werden muss.

Veränderungen in der phylogenetischen Diversität von Artengemeinschaften können trophische Interaktionen sowie Ökosystemfunktionen und –prozesse beeinflussen. Ob intensivere Landnutzung zu eine Abnahme der phylogenetischen Diversität hat, ist daher eine wichtige ökologische Frage der in dieser Dissertation genauer nachgegangen werden soll. Im ersten Kapitel gebe ich zuerst eine allgemeine Einführung in die Thematik des Forschungsfeldes phylogenetische Diversität. Danach widme ich mich den einzelnen Teilstudien und arbeite die Fragestellungen für diese Dissertation aus.

Im zweiten Kapitel wird der Frage nachgegangen ob in genutzten Grünländern die phylogenetische Diversität von Pflanzengemeinschaften entlang eines Landnutzungsintensitäts-gradienten abnimmt und ob häufige und seltene Arten in ähnlicher Weise reagieren. Meine Ergebnisse zeigen, dass die phylogenetische Diversität nur schwach mit zunehmender Intensität der Landnutzung abnimmt. Gemeinschaften von häufigen und seltenen Pflanzenarten zeigen dabei keine eindeutigen Unterschiede. Unterschiede im Effekt der Landnutzung auf die phylogenetische Diversität ergaben sich jedoch zwischen den einzelnen untersuchten Regionen. Der schwache Zusammenhang zwischen Phylogenetischer Diversität und Landnutzung ist möglicherweise durch ein schwaches phylogenetisches Signal in funktionellen Merkmalen die mit der Landnutzung zusammenhängen zu erklären.

Im dritten Kapitel habe ich die Zusammenhänge zwischen Pflanzendiversität, Landnutzung und der Diversität von herbivoren Insekten näher untersucht. Zuerst habe ich geprüft, ob die phylogenetische Diversität von Pflanzen neben der Artenanzahl ein besserer oder zusätzlicher Prädiktor der Insektendiversität ist. Weiterhin habe ich untersucht, ob es einen positiven Zusammenhang zwischen phylogenetischer Diversität der Pflanzen und herbivoren Insekten gibt. Und zuletzt habe ich geprüft, ob die phylogenetische Diversität von herbivoren Insekten mit zunehmender Intensität der Landnutzung abnimmt. Meine Ergebnisse zeigen, dass die Artenanzahl der Pflanzen ein guter Prädiktor für die Artenzahl der Insekten ist, die phylogenetische Diversität der Pflanzen darüber hinaus aber nur einen kleinen Teil der Variabilität der Artenanzahl von Insekten erklärt. Die phylogenetische Diversität der herbivoren Insekten zeigte sowohl mit der phylogenetischen Diversität der Pflanzen als auch mit der Landnutzung keinen eindeutigen Zusammenhang. Die Wirtspflanzen der herbivoren Insekten gehören meist einigen mehr oder weniger engen Gruppen innerhalb der kompletten Pflanzenphylogenie an (geclusterte Spezialisierung). Dadurch kann es zur Überschätzung der verfügbaren und genutzten Nischen innerhalb der Pflanzengemeinschaften kommen, wenn auch Pflanzengruppen mit in die Analyse einbezogen werden, die nicht oder kaum von den Insekten genutzt werden. Der fehlende Zusammenhang zwischen Landnutzung und phylogenetischer Diversität von herbivoren Insekten könnte mit einem schwachen oder nicht vorhandenem phylogenetischen Signal in landnutzungssensitiven Artenmerkmalen. Dadurch kann es zu keiner Selektion durch die Landnutzung kommen und wenn Arten verloren gehen, geschieht das eher zufällig.

Im vierten Kapitel habe ich die Auswirkungen der Landnutzung und der phylogenetischer Diversität von Pflanzengemeinschaften auf das Ausmaß der Invertebraten-Herbivorie untersucht. Ich prüfte, ob die Herbivorie mit steigender phylogenetischen Diversität der Pflanzen zunimmt und, ob Landnutzung einen direkten negativen Effekt auf die Herbivorie hat oder einen indirekten über Veränderungen in der Pflanzendiversität. Meine Ergebnisse zeigen eine signifikante Zunahme der Herbivorie mit zunehmender phylogenetischer Diversität. Weiterhin konnte ich zeigen, dass die Landnutzung zwar generell einen direkten negativen Effekt auf die Herbivorie hat, die Stärke der einzelnen Effekte sich aber zwischen den einzelnen Regionen unterscheiden.

Appendix Chapter 2

APPENDIX S1

Phylogenetic tree of the 282 vascular plant species sampled in the three regions in Germany between 2009 and 2011. Scale in *mya*.


50
Colchicum autumnale
Platanthera bifolia
Orchis militaris
Allium scorodoprasum
Allium vineale
Allium oleraceum
Allium sphaerocephalon
Muscari neglectum
Luzula campestris
Juncus articulatus
Juncus inflexus
Juncus effusus
Carex ovalis
Carex spicata
Carex flacca
Carex praecox
Carex caryophyllea
Carex montana
Carex hirta
Carex acutiformis
Glyceria fluitans
Brachypodium pinnatum
Bromus erectus
Bromus inermis
Bromus commutatus
Bromus hordeaceus
Briza media
Phalaris arundinacea
Calamagrostis canescens
Agrostis capillaris
Agrostis stolonifera
Arrhenatherum elatius
Trisetum flavescens
Koeleria pyramidata
Koeleria macrantha
Anthoxanthum odoratum
Poa annua
Poa trivialis
Poa pratensis
Poa angustifolia
Phleum pratense
Phleum bertolonii
Alopecurus pratensis
Alopecurus geniculatus
Helictotrichon pratense
Alopecurus pratensis
Deschampsia cespitosa
Holcus lanatus
Festuca arundinacea
Festuca pratensis
Festuca rubra
Lolium perenne
Lolium multiflorum
Lolium loliaceum
x Festulolium loliaceum
Festuca ovina
Festuca guestfalica
Festuca nigrescens
Festuca rubra
Dactylis glomerata
Cynosurus cristatus
Cynosurus pubescens
Helictotrichon pubescens
Pulsatilla vulgaris
Ranunculus ficaria
Ranunculus auricomus
Ranunculus acris
Ranunculus repens
Ranunculus bulbosus
Ranunculus tridactylites
Saxifraga tridactylites
Saxifraga granulata
Viola arvensis
Viola hirta
Hypericum perforatum
Euphorbia helioscopia
Euphorbia verrucosa
Euphorbia cyparissias
Linum catharticum
Genista tinctoria
Genista sagittalis
Anthyllis vulneraria
Hippocrepis comosa
Lotus corniculatus
Astragalus glycyphyllos
Medicago lupulina
Medicago x varia
Melilotus altissimus
Ononis spinosa
Ononis repens
Trifolium dubium
Trifolium campestre
Trifolium arvense
Trifolium alpestre
Trifolium medium
Trifolium pratense
Trifolium montanum
Trifolium repens
Vicia tetrasperma
Vicia hirsuta
Vicia cracca
Vicia tenuifolia
Vicia sepium
Vicia sativa
Lathyrus linifolius
Lathyrus angustifolius
Lathyrus nissolia
Lathyrus tuberosus
Lathyrus pratensis
Polygala comosa
Polygala vulgaris
Euphorbia amygdaloides
Euphorbia dulcis
Euphorbia cyparissias
Rosa canina
Rosa rubiginosa
Rosa arvensis
Potentilla reptans
Potentilla erecta
Potentilla argentea
Potentilla tabernaemontani
Potentilla verna
Potentilla micrantha
Potentilla anserina
Agrimonia eupatoria
Agrimonia procera
Agrimonia gryposepala
Filipendula ulmaria
Filipendula vulgaris
Alchemilla monticola
Alchemilla xanthochlora
Alchemilla vulgaris agg.
Aphanes arvensis
Aphanes inexpectata
Sanguisorba officinalis
Sanguisorba minor
Sanguisorba dodecandra
Circaea lutetiana
Epilobium hirsutum
Epilobium parviflorum
Epilobium montanum
Epilobium ciliatum
Epilobium tetragonum
Epilobium obscurum
Epilobium palustre
Epilobium roseum
Epilobium angustifolium
Oenothera biennis agg.
Chamaenerion angustifolium
Circaea lutetiana
Hippuris vulgaris
Myriophyllum spicatum
Myriophyllum verticillatum
Myriophyllum alterniflorum
Callitriche palustris agg.
Callitriche stagnalis
Callitriche hamulata
Callitriche platycarpa
Callitriche cophocarpa
Callitriche obtusangula
Callitriche hermaphroditica
Callitriche brutia
Callitriche stagnalis
Callitriche palustris agg.
Callitriche hamulata
Callitriche platycarpa
Callitriche cophocarpa
Callitriche obtusangula
Callitriche hermaphroditica
Callitriche brutia
Hippuris vulgaris
Myriophyllum spicatum
Myriophyllum verticillatum
Myriophyllum alterniflorum
Callitriche palustris agg.
Callitriche stagnalis

TABLE S2

Phylogenetic signal in 7 traits considered as sensitive to land use for all, common and rare species in the three regions (ALB: Schwäbische Alb, HAI: Hainich-Dün and SCH: Schorfheide-Chorin) and in all regions combined. SLA: specific leaf area; N: soil nutrient indicator value; M: mowing tolerance; G: grazing tolerance; T: trampling tolerance. Significant values are in bold.

		All species		Common species		Rare species	
		K	λ	K	λ	K	λ
SLA	ALL	0.099	**0.297**	0.138	<0.001	0.097	**0.182**
	ALB	**0.165**	**0.208**	0.172	0.081	**0.16**	0.175
	HAI	0.075	<0.001	0.143	<0.001	0.074	<0.001
	SCH	0.1	<0.001	0.12	<0.001	0.115	<0.001
log(max height)	ALL	**0.167**	**0.636**	**0.267**	**0.735**	**0.297**	**0.93**
	ALB	**0.158**	**0.712**	0.309	**0.855**	0.135	**0.646**
	HAI	**0.188**	**0.665**	**0.42**	**0.726**	**0.172**	**0.603**
	SCH	**0.238**	**0.614**	**0.886**	**0.805**	**0.238**	**0.531**
Flowering onset	ALL	**0.209**	**0.702**	0.108	<0.001	**0.226**	**0.643**
	ALB	**0.236**	**0.619**	0.091	<0.001	**0.252**	**0.546**
	HAI	**0.229**	**0.716**	0.086	<0.001	**0.254**	**0.69**
	SCH	**0.177**	**0.483**	0.164	<0.001	**0.194**	**0.421**
N	ALL	0.086	**0.192**	0.213	0.052	**0.141**	0.147
	ALB	0.07	0.254	0.207	0.143	0.147	0.263
	HAI	0.062	<0.001	0.15	<0.001	0.12	0.025
	SCH	0.127	<0.001	0.204	<0.001	0.156	<0.001
M	ALL	0.109	**0.287**	0.152	<0.001	**0.138**	**0.153**
	ALB	0.102	**0.356**	0.114	<0.001	**0.174**	**0.271**
	HAI	0.094	**0.223**	0.144	<0.001	0.13	0.14
	SCH	**0.159**	**0.219**	0.14	<0.001	0.144	0.048
G	ALL	0.104	**0.461**	0.111	<0.001	**0.137**	**0.424**
	ALB	**0.15**	**0.647**	0.102	<0.001	**0.3**	**0.71**
	HAI	0.101	**0.425**	0.091	<0.001	0.145	**0.437**
	SCH	0.112	0.191	0.191	<0.001	0.141	**0.282**
T	ALL	**0.105**	**0.223**	0.187	<0.001	0.122	**0.121**
	ALB	0.109	**0.335**	0.178	<0.001	0.137	0.232
	HAI	0.093	**0.167**	0.164	<0.001	0.115	0.14
	SCH	**0.147**	**0.148**	0.186	<0.001	**0.178**	0.149

APPENDIX S3

Mean (±SE) values and regression slopes of species richness for total, common and rare species assemblages in three regions in Germany. Red circles and solid line: Schwäbische Alb; green squares and dashed line: Hainich-Dün; blue triangles and dotted line: Schorfheide-Chorin.

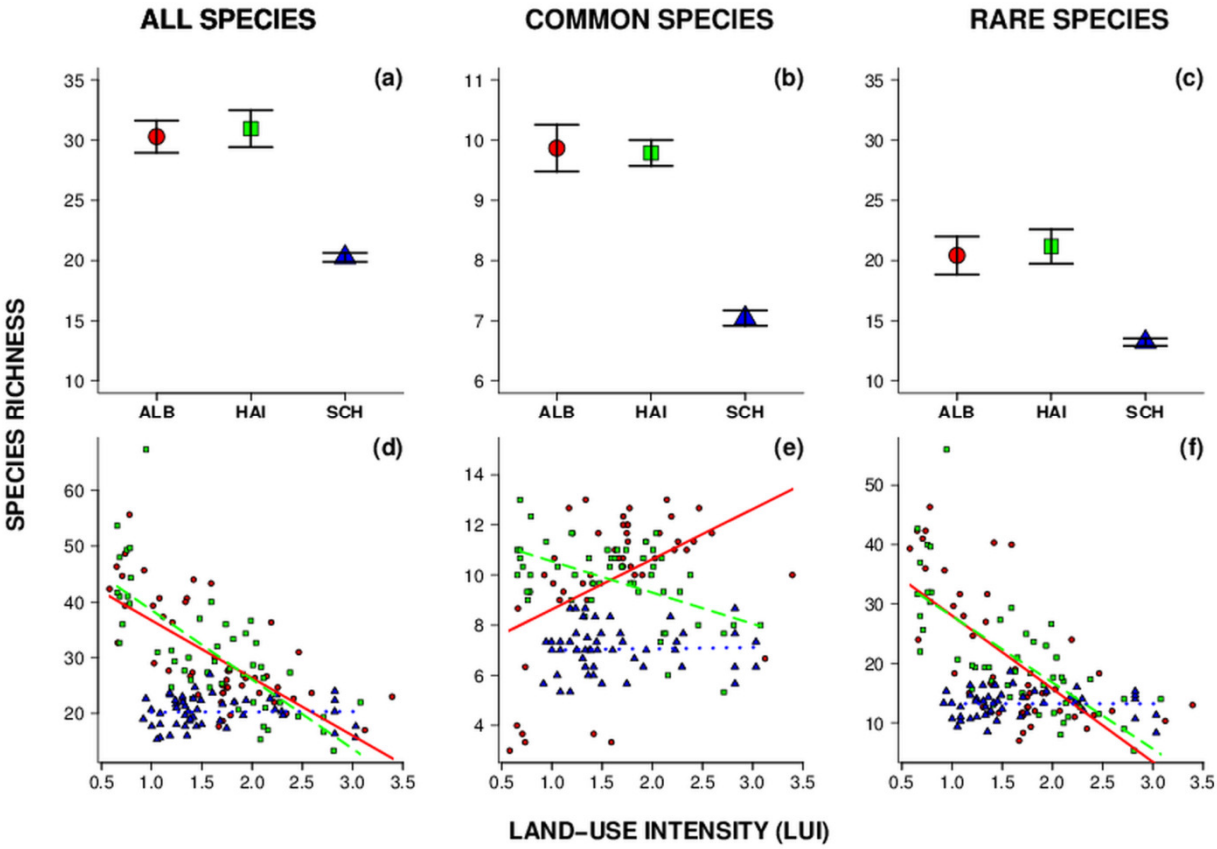


TABLE S4

Correlation coefficients of species richness, MPD and MNTD of all, common and rare species and LUI in the three regions (ALB: Schwäbische Alb, HAI: Hainich-Dün and SCH: Schorfheide-Chorin) and in all regions combined.

SPECIES RICHNESS

	ALL	COMMON	RARE
ALL	0.51 ***	0.06	-0.54 ***
ALB	-0.68 ***	0.45 ***	-0.68 ***
HAI	-0.74 ***	-0.53 ***	-0.72 ***
SCH	0.02	0.03	0.01

MPD

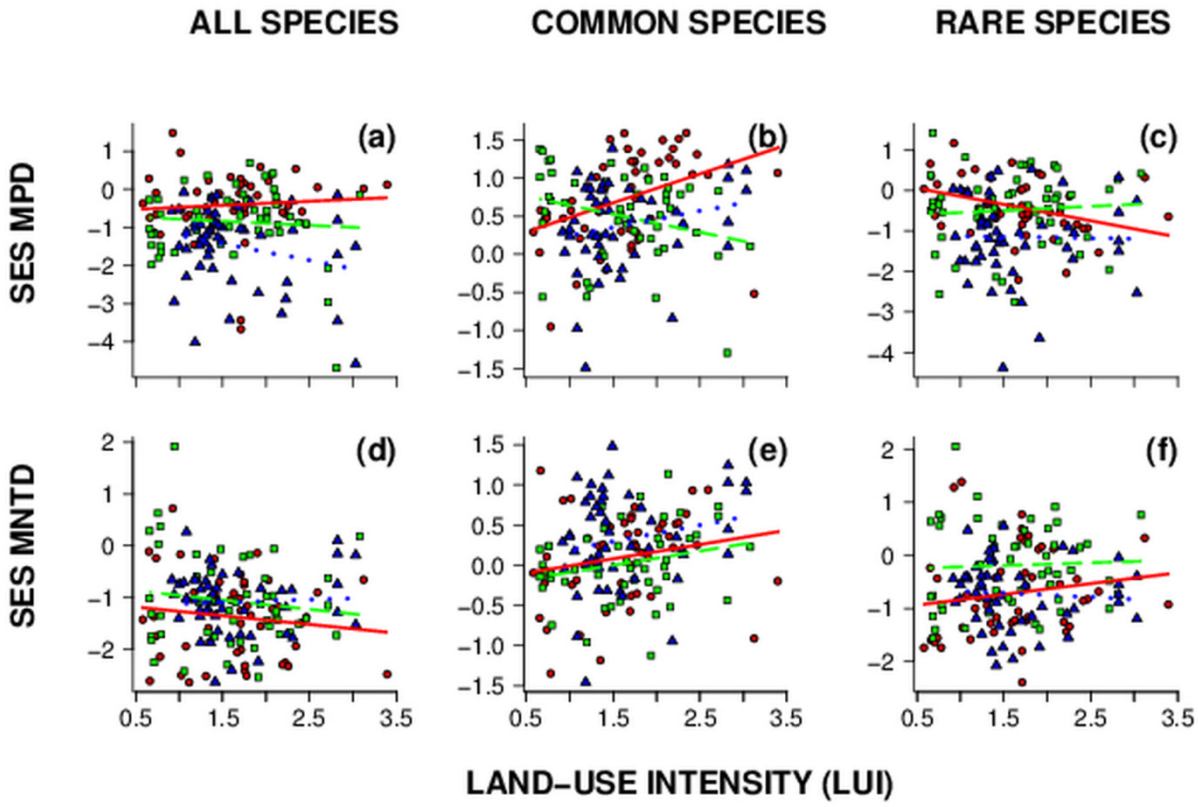
	ALL	COMMON	RARE
ALL	-0.15 .	-0.009	-0.15 .
ALB	-0.13	0.03	-0.03
HAI	-0.07	0.004	-0.07
SCH	-0.3 *	-0.08	-0.33 *

MNTD

	ALL	COMMON	RARE
ALL	-0.2 *	-0.08	0.09
ALB	-0.39 **	-0.12	0.15
HAI	-0.08	-0.01	0.29 *
SCH	-0.12	-0.15	-0.26 .

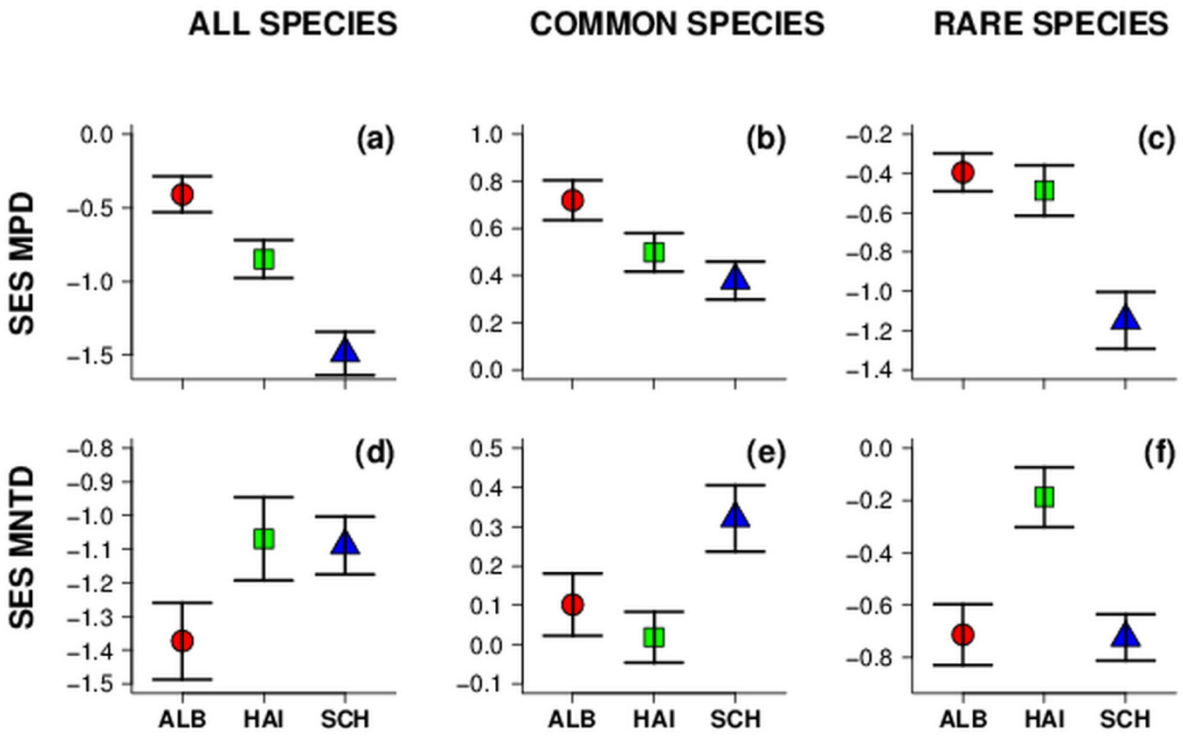
APPENDIX S5

Relationships between presence/absence based mean pairwise distance (effect size MPD), mean nearest taxon distance (effect size MNTD) and land-use intensity (LUI) in three regions in Germany. Red circles and solid line: Schwäbische Alb; green squares and dashed line: Hainich-Dün; blue triangles and dotted line: Schorfheide-Chorin.



APPENDIX S6

Mean (±SE) values of presence/absence based MPD and MNTD effect sizes for total, common and rare species assemblages in three regions in Germany. Red circles: Schwäbische Alb; green squares: Hainich-Dün; blue triangles: Schorfheide-Chorin.



Appendix Chapter 3

APPENDIX S1

SAMPLING, MOLECULAR METHODS AND PHYLOGENY RECONSTRUCTION

During the years 2008 to 2011 150 plots in the three regions were sampled using sweep-netting. Species were identified and stored in 70% ethanol until DNA extraction. Dry specimens from private collections were used where ethanol samples were not available. Additionally, DNA sequences were obtained from NCBI (GenBank). DNA from ethanol and dry specimens was extracted from legs and/or hemelytra following standard protocols.

Two regions from nuclear and mitochondrial genes (18S SSU rDNA [18S] and cytochrome c oxidase 1 mtDNA [CO1], respectively) were amplified and sequenced. For 18S two overlapping regions were amplified using primer pairs 3F-18 Sbi and 5F-9R (Schuh et al. 2009). For CO1 the primer pair LCO1490 and HCO2190 was used. Polymerase chain reaction (PCR) was carried out on Mastercycler® (Eppendorf) using 25µl PCR reaction mix. The PCR reaction mix contained 2µl $MgCl_2$, 2µl Taq Buffer, 1 µl dNTP (10 mM), 0.1µl of each primer, 0.2µl Polymerase (5 U/µl, Fermentas) 3µl DNA and 16.6µl water. PCR of 18S DNA started with denaturation at 95°C for four minutes followed by 35 cycles of denaturation at 94°C for 45 sec, annealing at 49°C for 45 sec and extension for one minute at 72°C. Last elongation step was performed at 72°C for seven minutes. For CO1 the initial denaturation was carried out at 94°C for five minutes and the last elongation was performed at 72°C for eight minutes.

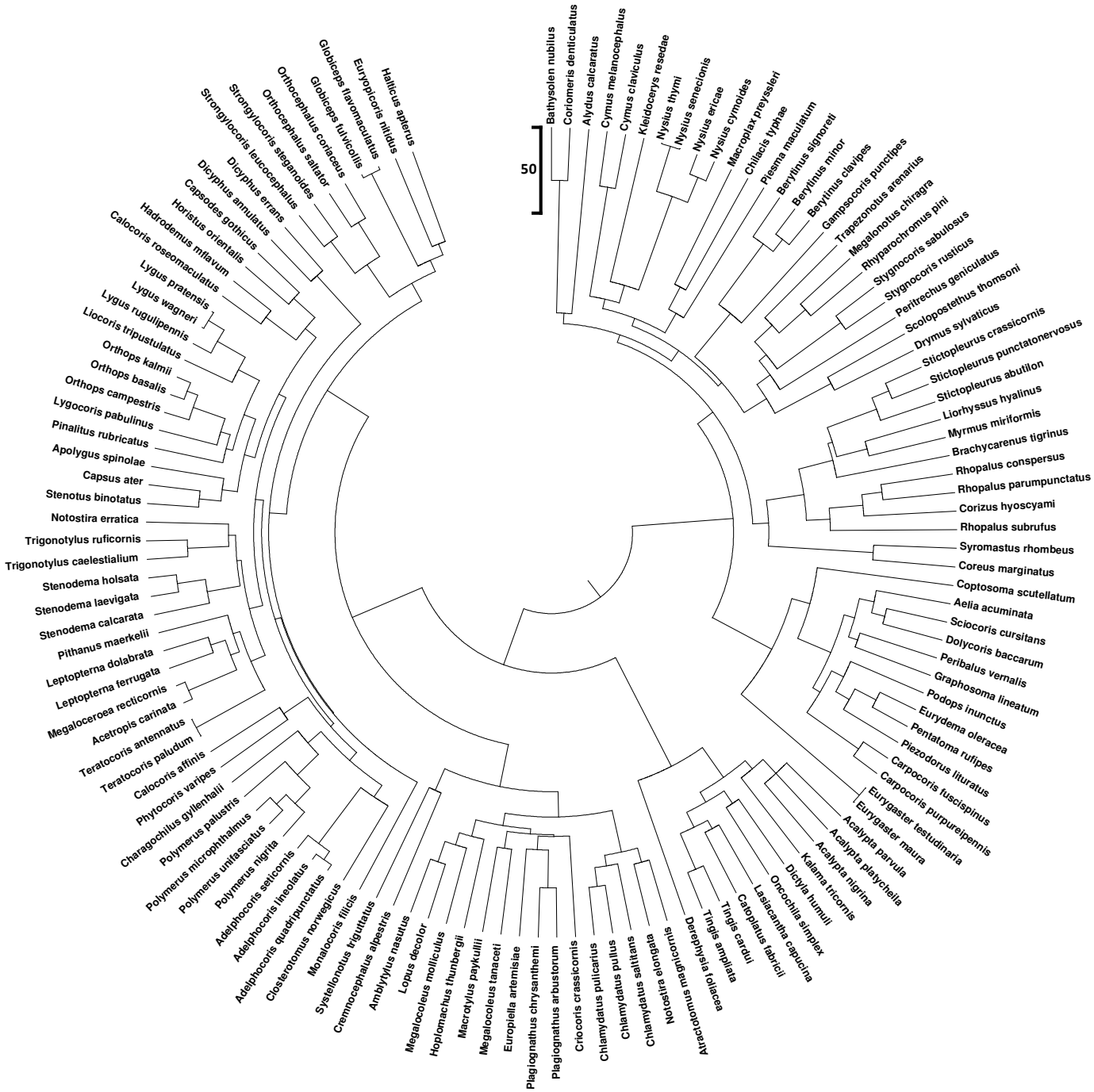
PCR products were visualized on 1.5% agarose gels and sent for sequencing to an external company (LGC genomics).

Forward and reverse sequences were manually checked with CodonCode alignment software (CodonCode, Dedham, MA, USA). Sequences were aligned with the online version of MAFFT (Katoh et al. 2002; Katoh et al. 2005) using the G-INS-i algorithm for 18S and FFT-NS-i algorithm for CO1 sequences using *Philaenus spumarius* (*Cicadomorpha, Aphrophoridae*) as outgroup. We used the online version of BEAST 1.8.1 within the CIPRES Science Gateway (Miller et al. 2010) to generate a maximum likelihood tree using the two gene partitions. The tree was generated using the two partitions with a HKY+G substitution model for 18S partition and GTR+G for COI partition. The substitution models were calculated using MEGA 6 (Tamura et al. 2013). We fixed the root to 251+-7 Mio years based on the earliest Heteroptera fossil (*Paraknightia magnifica*, Grimaldi 2005). For several species it was not possible to retrieve both DNA sequences. However, if they had only one congener, we put them as a sister group to them in the topology. Similarly we included species with two congeners as a polytomy. We used the bladj algorithm in PHYLOCOM to assign node ages and branch lengths to the new clades (Webb et al. 2008). The obtained ultrametric tree was used for the subsequent analyzes.

Butterflies were collected in a total of 136 plots in the three study regions in 2009. Sequences for the assessment of phylogenetic relationships were obtained from GenBank and included two nuclear markers (EF1-alpha, Wgl) and four mitochondrial markers (16s rRNA, COI, NDH1, NDH5). Sequences were aligned using BioEdit (Tom Hall, Ibis Therapeutics, Carlsbad, CA, USA) and MAFFT (Katoh et al. 2002; Katoh et al. 2005). A bayesian chronogram was constructed in BEAST 1.6.1 (Drummond et al. 2012). For detailed reconstruction method see Pellissier et al. (2013a). The obtained chronogram was ultrametrized using the chronos function in the R package ape (Paradis et al. 2004). A lambda value of 5 was assessed using the cross-validation procedure in the same package. The obtained ultrametric tree was used in the subsequent analyzes.

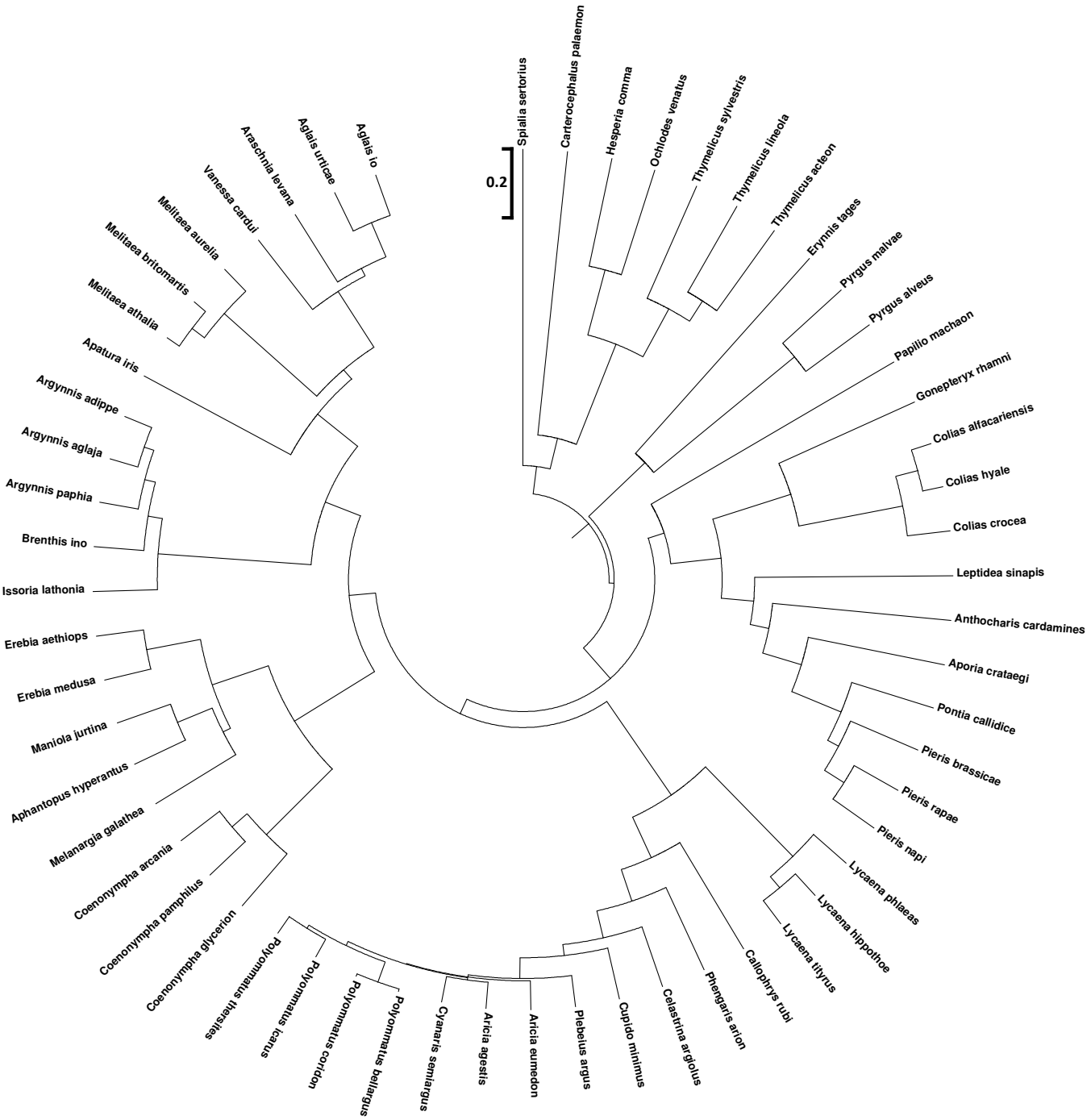
APPENDIX S2

Phylogenetic tree of the 133 true bug species used in this analysis. Scale in *mya*.



APPENDIX S3

Phylogenetic tree of the 58 butterfly species used in this analysis. Scale in substitutions per side.



APPENDIX S4

Effects of region, plant species richness, plant phylogenetic diversity and LUI on insect herbivore (a) species richness and (b) phylogenetic diversity in the three regions in Germany. ANOVA tables of the models with bold numbers indicating significant effects. The tables (a) and (b) are counterparts of the tables 1 and 2, respectively, showing results based on abundance weighted measures of phylogenetic diversity.

(a)

	TRUE BUGS					BUTTERFLIES				
	Df	**SS**	**MSS**	**F**	***p***	**Df**	**SS**	**MSS**	**F**	***p***
Region	2	154.12	77.06	4.439	0.013	2	176.14	88.07	12.05	**<0.0001**
Plant SR	1	611.49	611.49	35.2251	**<0.0001**	1	449.71	449.71	61.54	**<0.0001**
Plant SES MPD	1	16.90	16.90	0.9736	0.33	1	20.67	20.67	2.83	*0.095*
Plant SES MNTD	1	37.99	37.99	2.1883	0.14	1	8.19	8.19	1.12	0.29
LUI	1	14.58	14.58	0.8397	0.36	1	31.92	31.92	4.37	**0.039**
LUI x Plants SR						1	16.02	16.02	2.19	0.14
LUI x Plants SES MPD						1	8.04	8.04	1.10	0.30
LUI x Plants SES MNTD						1	0.53	0.53	0.07	0.79
Residuals	143	2482.42	17.36			124	906.06	7.31		

(b)

	MPD					MNTD				
Heteroptera										
	Df	**SS**	**MSS**	**F**	***p***		**Df**	**SS**	**MSS**	**F**	***p***
Region	2	32.099	16.05	24.67	**<0.0001**	Region	2	2.18	1.09	5.07	**0.0074**
Plant SR	1	0.369	0.37	0.57	0.45	Plant SR	1	1.66	1.66	7.73	**0.0061**
Plant SES MPD	1	0.463	0.46	0.71	0.40	Plant SES MNTD	1	0.11	0.11	0.51	0.48
LUI	1	0.103	0.10	0.16	0.69	LUI	1	0.11	0.11	0.53	0.47
Residuals	144	93.698	0.65			Residuals	144	30.91	0.21		
Lepidoptera										
	Df	**SS**	**MSS**	**F**	***p***		**Df**	**SS**	**MSS**	**F**	***p***
Region	2	12.39	6.20	6.12	**0.0029**	Region	2	1.20	0.60	0.72	0.49
Plant SR	1	2.48	2.48	2.45	0.12	Plant SR	1	2.93	2.93	3.52	*0.06*
Plant SES MPD	1	2.20	2.20	2.17	0.14	Plant SES MNTD	1	0.57	0.57	0.69	0.41
LUI	1	0.05	0.05	0.05	0.82	LUI	1	0.31	0.31	0.38	0.54
Residuals	128	129.70	1.01			Residuals	128	106.51	0.83		

APPENDIX S5

Correlations (Spearman's r) between phylogenetic diversity (MPD (P/A); MPD (ABUND); MNTD (P/A); MNTD (ABUND)) of two groups of herbivorous insects and plant traits (specific leaf area (SLA; in cm^2/g), maximum height (cm), start of flowering (month of the year), soil nutrient indicator value (N), mowing tolerance (M), grazing tolerance (G) and trampling tolerance (T)). λ indicates the phylogenetic signal present in the traits. For further information see Egorov et al. (2014). Bold numbers indicate significant correlations, italic numbers marginally significant.

	SLA	**Max height**	**Start flowering**	**N**	**M**	**G**	**T**
Lepidoptera	-0.06;*0.16* ;-0.008;**0.2**	-0.04;0.07;-0.13;0.002	-0.03;0.08;-0.1;-0.07	0.002;**0.24**;-0.01;**0.23**	0.02;**0.22**;0.05;**0.28**	0.13;**0.28**;*0.15* ;**0.25**	**0.19**;**0.3**;**0.2**;**0.26**
Heteroptera	**-0.25**;**-0.18**;**-0.32**;-012	**-0.18**;*-0.16* ;**-0.2**;**-0.2**	*-0.15* ;**-0.24**;-0.08;**-0.23**	**-0.28**;**-0.24**;**-0.29**;**-0.19**	**-0.28**;**-0.23**;**-0.32**;**-0.17**	**-0.23**;**-0.24**;-0.11;-0.09	*-0.16* ;**-0.2**;-0.08;-0.13
λ	**0.297**	**0.636**	**0.702**	**0.192**	**0.287**	**0.461**	**0.223**

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ERKLÄRUNG

Hiermit versichere ich, dass ich meine Dissertation mit dem Titel

„Community phylogenetics and invertebrate herbivory in managed grasslands"

selbstständig und ohne unerlaubte Hilfe verfasst habe. Ich bediente mich dabei keiner anderen als der von mir gekennzeichneten Quellen. Die Dissertation wurde in der jetzigen oder ähnlichen Form noch bei keiner anderen Hochschule eingereicht und hat keinen sonstigen Prüfungszwecken gedient.

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